COMPARATIVE BREEDING ECOLOGY IN ARCTIC-GEESE OF DIFFERENT BODY SIZE: AN EXAMPLE IN ROSS'S AND LESSER SNOW GEESE

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ABSTRACT

Two closely-related, different-sized species of geese nest sympatrically south of the Queen Maud Gulf (QMG) in Canada's central arctic. Following a period of high population growth rate in both species within the QMG, the population growth rate of larger-bodied lesser snow geese (*Chen caerulescens caerulescens*; hereafter snow geese) has slowed most recently to roughly half that observed in smaller-bodied Ross's geese (*Chen rossii*). I focused on factors that influence productivity and recruitment in these two species, to improve our understanding of life history variation associated with interspecific differences in body size, and to test for density-dependent population responses. I used long-term data (1991 to 2008) to compare spring nutrient reserves, breeding strategies, clutch sizes, nest success, and juvenile survival in Ross's and snow geese breeding at Karrak Lake, Nunavut; a large breeding colony located within the QMG.

Long-term patterns of spring body condition (i.e., fat and protein reserves) diverged in prospective breeding female Ross's and snow geese implying that differences in food acquisition ability had become more acute. Snow geese displayed larger reductions in protein and fat reserves through time compared to Ross's geese thereby suggesting a differential density-dependent response in the ability to store nutrient reserves, a prerequisite for breeding in both species. Decreased per capita food availability influenced the timing of reproduction in both species. Nesting phenologies of Ross's and snow geese, adjusted for variation in phenology of local spring climate, have become later by 6.5 and 5.0 days, respectively, since 1991. Nutritional strategies (i.e., reliance on reserves versus local food) used for clutch formation differed between species. Ross's geese displayed greater reliance on stored reserves (i.e., capital breeding) than did snow geese, though both used endogenous reserves ($\geq$ 62% of yolk protein, $\geq$ 48% of albumen, and $\geq$ 73% of yolk lipid) for clutch formation. Ross's and snow geese experienced declines of 28% and 23% in body masses from arrival to post-laying and also until hatch demonstrating that endogenous reserves are the main nutrient sources for incubation. Still, constraints of small size forced Ross's geese to use a mixture of local food plants and reserves for incubation metabolism.

I then examined differences in clutch size, nest success, and juvenile survival to understand of the role of recruitment in the interspecific divergence of population trajectories. I did not find strong interspecific differences in clutch size and nest success. Overall, snow geese had a larger mean clutch size, which was expected based on benefits of a larger-body size.

Clutch sizes decreased with delays in breeding and decreasing protein reserves of arriving females, although Ross's geese displayed larger declines with decreasing protein reserves. Mean apparent nest success for Ross's geese was 4.5% higher compared to snow geese. Nest success showed large declines (11%) in both species with increasing population size at the breeding colony. However, nest success of snow geese decreased twice as fast with delays in breeding compared to Ross's geese. Last, I found no evidence of negative density dependence in juvenile survival over time. Juvenile survival was higher in snow geese (48%) compared to Ross's geese (38%), consistent with a life history prediction based on body size differences. Despite lower juvenile survival, recruitment by Ross's geese is likely greater than that of snow geese because of earlier sexual maturity, higher breeding probability and/or greater nest success.

Ultimately, small body size of Ross's geese may produce an ideal life history schedule under resource limitation at this colony i.e., one that maximizes fitness compared to larger snow geese. Life history characteristics of Ross's geese (e.g., absolutely lower energy requirement, have a flexible breeding strategy, higher reproductive effort, an earlier age of sexual maturity, a shorter breeding cycle allowing delayed arrival and nest initiation on arctic breeding areas, and shorter time required by goslings to attain adult size), in addition to their smaller bill morphology may allow exploitation of a wider niche space (i.e., one that includes marginal quality and low quantity vegetation) relative to snow geese. Because there were no large differences in components of recruitment considered here, other components of recruitment (age of sexual maturity, breeding probability) may be affected more strongly by diminished spring nutrition in snow geese and thus have a larger influence on local population dynamics.

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Support and encouragement from many people and organizations made this project possible. I want to first thank my advisor, Dr. Ray Alisauskas, for all his guidance during my PhD tenure. I believe he has mentored me to become a better writer and scientist. I also thank him for the opportunity to conduct research at the Karrak Lake research station and co-manage research at Redberry Lake, SK on white-winged scoters. I would also like to express my sincere gratitude to the participants of my graduate committee: Drs. Bob Clark, Karen Machin, and Francois Messier; their expertise in varying areas and thought provoking questions made committee meetings very beneficial. Last, I would like to thank Dr. Joel Schmutz for serving as my external examiner, and for his thought provoking questions and insight during my defense.

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1. GENERAL INTRODUCTION

1.1 POPULATION DYNAMICS AND LIFE HISTORY VARIATION

Understanding how life history traits (age-specific reproduction and survival) affect population trends and identifying factors that regulate populations are major goals of population biology (Begon et al. 1996, Williams et al. 2002). Populations are affected by biotic and abiotic factors such as weather, food availability, predation, competition, disease, and quality and quantity of habitat (Lack 1954, Newton 1998, Williams et al. 2002). Consequently, populations fluctuate over time. Population fluctuations may result from changes in any or all components of life cycles such as adult survival or components of recruitment (e.g., offspring survival) (Caswell 2000). Thus, understanding ecological factors that influence specific vital rates can lead to an improved knowledge of processes responsible for population change.

Regarded as age-specific reproductive and survival rates, life history traits of organisms are generally considered a composite of variables with tradeoffs among them that act to maximize fitness under present ecological conditions (Stearns 1992). These traits highlight strategies associated with reproduction and survival such as age and size at maturity, number and size of offspring, and acquisition and allocation of resources (Stearns 1992). Collectively, life history traits have profound influences on population dynamics because they are predictably linked to vital rates (Heppell et al. 2000). For example, early age of sexual maturity increases reproductive rate (i.e., births) and ultimately intrinsic rate of population growth, but at a cost of increased adult mortality (Stearns 1992, Williams et al. 2002). In general, life history traits are expected to be less variable within species compared to among species since traits are mediated by differences in body size (Peters 1983, Blanckenhorn 2000, Dobson and Oli 2007). The principal axis of interspecific variation in life histories is the fast-slow continuum of population growth rate (Heppell et al. 2000, Ricklefs 2000, Saether and Bakke 2000). For example, smaller species require absolutely less energy and thus can reproduce sooner, which confers fecundity advantages (Peters 1983, Blanckenhorn 2000). On the other hand, larger species generally have delayed sexual maturity, lower fecundity, and higher survival because greater allocation to somatic growth in larger species represents a tradeoff with reproductive rate (Peters 1983, Futuyma 1998). Accordingly, body size influences population growth rate and among birds, waterfowl in particular, the potential for recruitment to influence population trajectory appears to

be greater for smaller species (Johnson et al. 1992, Saether et al. 1996, Ricklefs 2000). Ultimately, an understanding of how life history strategies influence population dynamics is critical for predicting how populations might respond to changing environmental conditions.

In avian species, life cycles are composed generally of breeding probability, nesting success, offspring survival to fledge, juvenile survival, subadult survival, and adult survival. Population growth rate (i.e., $\lambda_t=N_{t+1}/N_t$) is equivalent to the sum of adult survival probability and recruitment rate (Nichols and Hines 2002), whereby populations can decrease ($\lambda_t < 1$), increase ($\lambda_t > 1$) or remain constant ($\lambda_t = 1$) (Williams et al. 2002). However, the sensitivity of population growth rate to variations in demographic parameters can vary among species based on their placement within the fast-slow continuum i.e., adult survival is critical for slow species, while recruitment is essential to fast species (Saether and Bakke 2000). In many waterfowl species, adult survival probability has the greatest potential influence on population growth (Flint and Grand 1997, Rockwell et al. 1997, Schmutz et al. 1997, Hoekman et al. 2002). Even so, variation in recruitment can have important consequences for population change (Williams et al. 2002). Recruitment often exhibits marked interannual variation and, in turn, can become an important determinant of population growth rate (Nur & Sydeman 1999). Recruitment rate is defined as the product of breeding probability, clutch size, nesting success, and offspring survival to breeding age (i.e., offspring survival to fledge, juvenile survival, and subadult survival). When expressed as a proportion of population growth rate of breeding adults, this rate can also be defined as the probability of "entry" into the adult population.

1.2 SPECIES AND STUDY POPULATION

Ross's (*Chen rossii*) and lesser snow (*Chen caerulescens caerulescens*, henceforth snow geese) geese are two different-sized arctic-breeding geese that are closely related (99.7% similarity of DNA) (Avise et al. 1992, Hebert et al. 2004) and breed sympatrically within large colonies. The Ross's goose is the smallest of the North American light geese and is considered a smaller form (66% size) of the snow goose (Anderson et al. 1992). It is suspected that Ross's geese evolved their small body size during the previous glacial maximum (130,00-150,00 years ago) in the northern Canadian Arctic Archipelago, an area characterized by harsh climate, low productivity, and abbreviated summers (Ploeger 1968, MacInnes et al. 1989). By contrast, current populations of snow geese are believed to have evolved their larger size in east Siberia, Russia, an area

typified by highly productive tundra and a longer growing season (Ploeger 1968). However, the evolution of body size can be an antagonistic process dependent upon the annual cycle such that migration distances and wintering areas (food types) are also important in the evolution of body size (Owen and Black 1989). Regardless of how these species evolved, their interspecific differences in body sizes likely confer differences in life history attributes. In general, it is thought that Ross's geese are skewed toward the fast-side of the continuum, where small size yields a higher reproductive rate. On the other hand, larger-bodied snow geese are closer to the slow-side of the continuum compared to Ross's geese; in particular, adult survival of snow geese is considered the most important contribution to population growth rate (Rockwell et al. 1997).

Populations of arctic-breeding geese have increased dramatically in recent years (Boyd et al. 1982, Ankney 1996, Alisauskas et al. 2009). Exponential increase has been attributed to agricultural food subsidies on winter and migration areas (Alisauskas et al. 1988, Bateman et al. 1988, Alisauskas and Ankney 1992), lower harvest rates (Francis et al. 1992), migration refugia (Raveling 1978), and arctic climate amelioration (MacInnes et al. 1990). Consequently, large increases in size of several populations of North American geese have resulted in ecosystem-level increases in arctic herbivory (Batt 1997). Particularly, declines in quality and quantity of food resources at some colonies have led to decreases in clutch size and growth and survival of offspring as well as adult body size (Cooch et al. 1991b, Cooch et al. 2002, Alisauskas et al. 2006a). Thus, density-dependent competition for food could be contributing to population regulation by decreasing productivity and survival (Sinclair 1989).

Snow goose populations south of Queen Maud Gulf in Canada's central arctic grew at an annual rate of 16.7% from 1967 to 1988 while Ross's geese populations grew at only 7.9% per year during the same time period (Kerbes 1994). However, since then, Ross's geese have grown at 11.0% per year, a rate roughly double that shown by snow geese for the same time-period (Alisauskas et al. 2011a). Several mechanisms exist for this difference in population growth including interspecific differences in immigration and emigration, and variation in annual survival of adults or interspecific variation in local production of young and subsequent recruitment. Life history theory predicts that populations under nutritional stress display diminished rates of recruitment (Eberhardt 2002). Alisauskas (2002) suggested that long-term declines evident in age ratios (immature:adult) of snow geese harvested in the midcontinent of North America were a result of density dependence at the superpopulation level (i.e., the North

American population of snow geese), similar to patterns uncovered at local population scales (Cooch et al. 1991b). Harvest age ratios of Ross's geese are about twice as high as those for snow geese suggesting that Ross's geese may tend to have considerably higher recruitment than do snow geese (Moser and Duncan 2001). Density-dependent effects (i.e., regulating factors), from deteriorating habitat quality on arctic breeding areas, such as diminished adult body size, clutch size, and gosling growth and survival may be slowing population growth of snow geese not just at certain locales of their breeding range (Cooch et al. 1989, Cooch et al. 1991b, Francis et al. 1992), but over their entire breeding range (Alisauskas 2002). Density dependence is likely more severe in larger species via increased costs of a longer developmental time and fast growth and/or nutritional constraints due to absolutely higher energy requirements (Blanckenhorn 2000). On the other hand, Ross's geese may be closer to the minimum viable size for an arctic-breeding obligate avian herbivore, which relative to larger species, may lower the threshold at which forage conditions are considered poor; in this way, Ross's geese may reduce the likelihood of incurring negative population consequences under environmental conditions similar to those face by snow geese (Sedinger et al. 1998, Blanckenhorn 2000). Moreover, evidence suggests that Ross's geese are able to make use of breeding areas severely damaged by breeding snow geese whereas snow geese disperse to new habitats or remain and breed less efficiently (see above) (Ankney 1996, Cooch et al. 1993). In this way, Ross's geese may be able to exploit a wider niche space compared to snow geese, as communities of arctic vegetation deteriorate from combined effects of overgrazing by both species.

1.3 THESIS OBJECTIVES AND CHAPTER DESCRIPTIONS

Research in this thesis was motivated by a series of hypotheses associated with the influence of body size on the interspecific divergence in local population trajectories of Ross's and snow geese. To understand divergences in population trajectories, I examined differences in components of recruitment predicted by interspecific differences in body size. I focused on clutch size, nest success, and juvenile survival and how each responds to variation in ecological conditions shared by both species. Moreover, I also examined trends in adult body size and spring nutrition because of their importance to breeding success and recruitment in arctic geese. Finally, because studies that examined life history constraints generally focused on responses to the environment they overlooked the importance of physiology (i.e., metabolism, nutrition, and

thermal relationships) within the context of life history diversities (see Ricklefs and Wikelski 2002); I investigated species differences in nutritional strategies used in clutch formation. By studying these closely-related, yet different-sized, species simultaneously, I aimed to understand the interplay of response to environmental conditions with respective body sizes (Sandercock et al. 2005). The ecological cause for differences in vital rates between species is unknown, although differences likely result from constraints of an organism's life history traits (tradeoffs among them or physiological constraints) (Nagy 1987, Stearns 1992).

I have organized this thesis into four data chapters, a synthesis, and appendix. The data chapters were written as independent manuscripts for publication in peer-reviewed journals. Hence, there are redundancies in sections of different chapters. The four major components of this thesis are outlined briefly below.

Endogenous nutrient stores of arctic-breeding geese arriving onto breeding colonies are particularly important since they significantly influence clutch size (Ryder 1970, Ankney and MacInnes 1978, Sedinger et al. 1995, Bon 1997, but see Choinière and Gauthier 1995) and are essential for meeting metabolic demands of incubation when local foods are unavailable or very scarce (Ankney and MacInnes 1978, Choinière and Gauthier 1995, Gloutney et al. 2001). A factor critical to the amount of stored reserves an individual can transport is its body size (Ankney and MacInnes 1978). Systemic declines in body size of adult geese may act to decrease reproductive output because it leads to an absolute reduction in the capacity to carry nutrient reserves. Ultimately, annual variation in levels of pre-breeding nutrient reserves can influence population dynamics (Alisauskas 2002). For those reasons, the primary objective for chapter 3 was to examine changes in adult body size and spring nutritional condition of Ross's and snow geese. My first objective was to assess whether a long-term decline in adult body size (Alisauskas 2002) has continued (1991 to 2008). The second objective was to assess long-term (1993 to 2008) changes in stored nutrient reserves (fat and protein) of female geese of both species as they arrived to breed at Karrak Lake and examine the importance of year, population size, timing of reproduction, spring weather, and the spring conservation hunt to nutrient reserves.

Understanding nutrient dynamics during reproduction can provide insight regarding life history variation since the manner in which animals use their food supply can have significant consequences for fitness (Stearns 1992). The factors that influence breeding performance can be

different between species that rely on stored food or breeding ground forage (Choinière and Gauthier 1995, Alisauskas 2002, Fèret et al. 2003). Breeding strategies (i.e., nutritional strategies) among waterfowl, ultimately, represent a tradeoff between nutrients available for clutch formation and incubation (Alisauskas and Ankney 1992a). Hence, in chapter 4, the primary objective was to examine breeding strategies of Ross's and snow geese by assessing the importance of endogenous (capital; body reserves) and exogenous (income; local forage) nutrients to clutch formation. The first objective was to examine variation in breeding strategies of Ross's and snow geese by estimating proportional contributions of endogenous and exogenous nutrients to first and last-laid egg components of a clutch, inferred from stable isotope analysis of eggs, tissues and foods of female geese (Gauthier et al. 2003). Then, I addressed the use and importance of staging area foods by comparing breeding strategies and isotopic signatures of tissues and eggs from birds that recently arrived onto the colony with those that had commenced incubation. Finally, I examined interspecific differences in mass change of goose tissues during breeding (arrival to hatch) to estimate absolute supply of endogenous nutrients. However, as my research in Chapter 4 progressed, I identified a problem with currently applied discrimination factors, from somatic reserves to egg components, used in estimation of breeding strategies (i.e., non-convergence of isotopic models with discrimination factors from the carnivore model; Hobson 1995). Consequently, this led to an Appendix in which I examined the sensitivity of breeding strategy results with a range of plausible discrimination factors. I discuss the efficacy of currently used discrimination factors, from the carnivore model, for capital breeders (i.e., birds relying on somatic reserves for egg production) (Hobson 1995).

Clutch size is a critical determinant of recruitment in birds (Lessells 1986, Johnson et al. 1992) and variation in clutch size of colonial geese that breed in the arctic is governed primarily by arrival body condition (Ryder 1970, Ryder 1972, Ankney and MacInnes 1978, Hamann and Cooke 1987, MacInnes and Dunn 1988). Likewise, density-dependent declines in per capita food resources on spring staging areas may be a relatively new proximate factor impinging on the ability to store reserves with concurrent reductions in clutch size because of the recent extreme growth of some arctic-breeding goose populations (Cooch et al. 1989, Cooke et al. 1995, Sedinger et al. 1998). On the other hand, nest success (the probability that at least one egg hatches in a nest) can also be a bottleneck for recruitment (Cowardin and Blohm 1992, Johnson et al. 1992, Hoekman et al. 2002), and can be influenced by numerous ecological factors that

influence the likelihood with which nests are depredated, abandoned, or destroyed (Afton and Paulus 1992, Flint and Grand 1996). Predation is the most important proximate cause of nest failure in birds (Martin 1995), although failure by arctic-breeding geese to store sufficient nutrient reserves for high nest attendance and completion of incubation may lead to increased predation. For example, studies suggest that nest success of arctic geese is predictably higher for nests initiated earlier in the season or in benign weather conditions, given that later nesting birds are likely in poorer condition and inclement weather increases use of somatic reserves (Ankney and MacInnes 1978, Raveling 1989) leading to reductions in nest attendance and increased likelihood of predation. Primary objectives for chapter 5 were to examine long-term (1993 to 2008) changes in clutch size and nest success of Ross's and snow geese in relation to timing of reproduction, spring nutrition, local weather conditions, nesting densities, and nesting habitat.

Juvenile survival, i.e., survival from fledging until one year later, is another component of recruitment, and can be particularly important because it is a prime determinant of the proportion of new individuals entering a breeding population (Cooch et al. 2001, Reed et al. 2003). Juvenile survival can be modified by many interacting ecological, biological and physiological factors, though it is often linked to local environment conditions during development (Todd et al. 2003). Consequently, knowledge of factors that influence juvenile survival can reveal probable mechanisms of population change. Thus, in chapter 6, the main objective was to examine long-term (1991 to 2004) changes in juvenile survival in Ross's and snow geese. I was also interested in estimation of the consequences of late nesting and the role that inclement weather plays in governing juvenile survival since little is known about how different sized congeners respond in the same but variable ecological conditions on their breeding grounds.

Chapter 7 is a synthesis in which I discuss my main findings from the thesis. I address the question "could differences in population trajectory be related to (a) the influence of environmental factors on demographic variables, (b) an ecological process (i.e., food acquisition), or (c) potential differences in adaptations to arctic-breeding (i.e., differential resource allocation or timing of breeding) brought about by variation in life history traits?" Ultimately, life history constraints associated with small body size of Ross's geese (income-biased reproductive strategy, delayed arrival on arctic breeding areas, and increased reproductive effort) may allow more favorable outcomes compared to snow geese in areas of resource limitation.

2. STUDY AREA

This study was conducted at the Karrak Lake goose colony located in Nunavut, Canada (67° 14' N, 100° 15' W) during the breeding seasons 1991-2008 (Fig. 2.1). This colony is the largest known colony in the Queen Maud Gulf Migratory Bird Sanctuary with about equal representation of each species (Kerbes 1994). Approximately 40% of the continental Ross's goose population nests there, while almost the entire Ross's goose and ~15% of the snow goose population nests in the sanctuary (Kerbes 1994). Areas up to 70 km north of Karrak Lake constitutes primary brood-rearing habitat for both Ross's and snow geese produced at Karrak Lake (Slattery and Alisauskas 2007) and is composed of a heterogeneous mosaic of sedge meadows, tundra ponds, and rock outcrops (Ryder 1972, Didiuk and Ferguson 2005). Since research began at Karrak Lake in the 1960's, populations of geese have grown geometrically from 17,000 in 1965, to ~463,000 in 1993 (Kerbes 1994), and to 1.2 million individuals in 2008 (Fig. 2.2). Hence, this long-term study was conducted during a time of significant geometric colony growth. Moreover, geese have maintained high levels of nesting density (~5000 nests per km^2) (Ryder 1969, Alisauskas unpubl. data) encompassing ~ 200 km^2 of terrestrial habitat (Alisauskas unpubl. data). This population of a very dense concentration of nesting geese has caused a large reduction in species richness and diversity of vegetation within the colony such that low digestible forage remains for consumption (Gloutney et al. 2001, Alisauskas et al. 2006a). Additionally, the colony is surrounded by a biodeterioration zone such that the protein content of graminoids increases farther from the periphery of the colony (Slattery 2000).

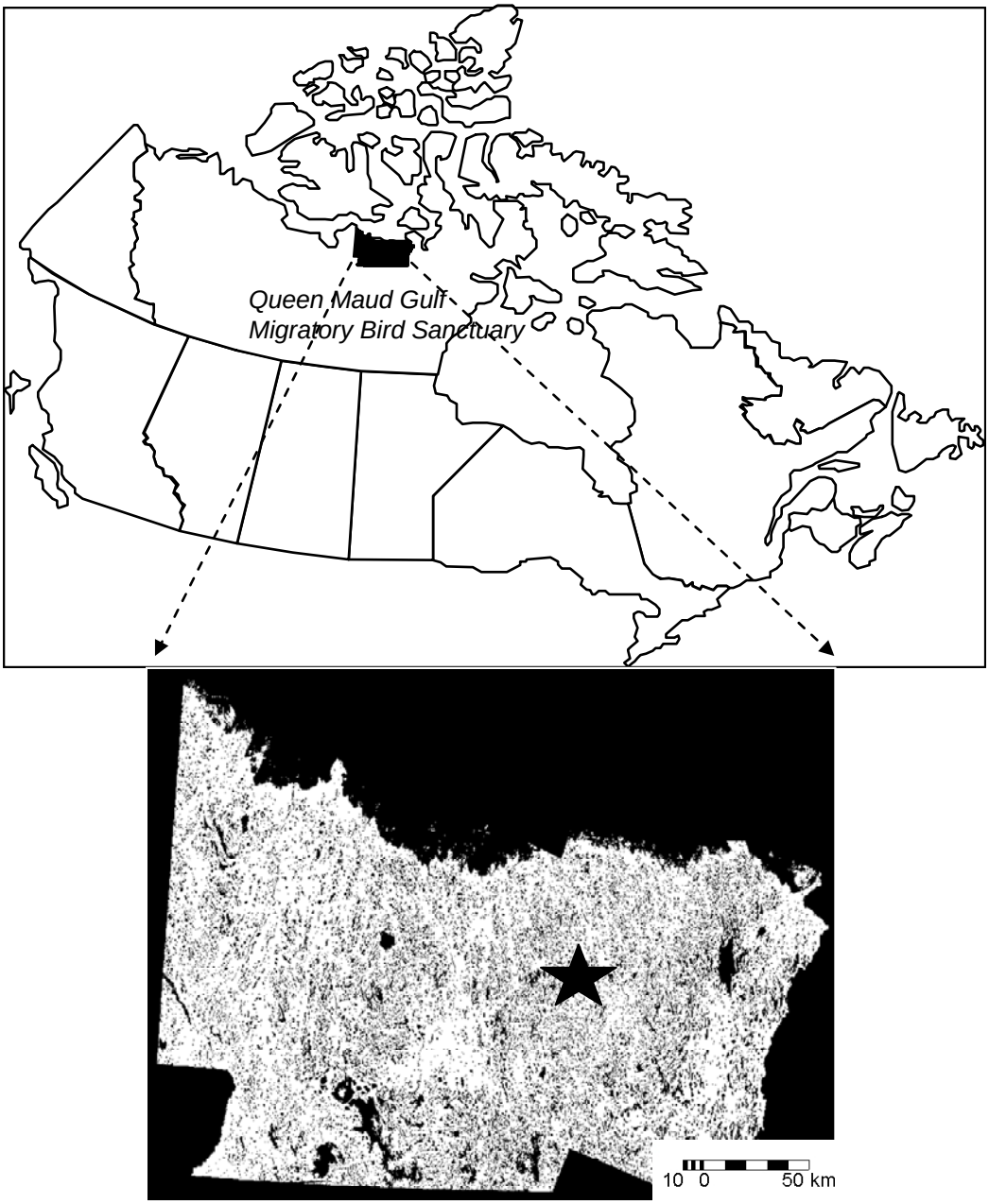


Figure 2.1. Location of the Karrak Lake light goose colony within the Queen Maud Gulf Migratory Bird Sanctuary (QMGMBS), Nunavut, Canada. The shaded area indicates the QMGMBS and the star delineates the location of the Karrak Lake colony.

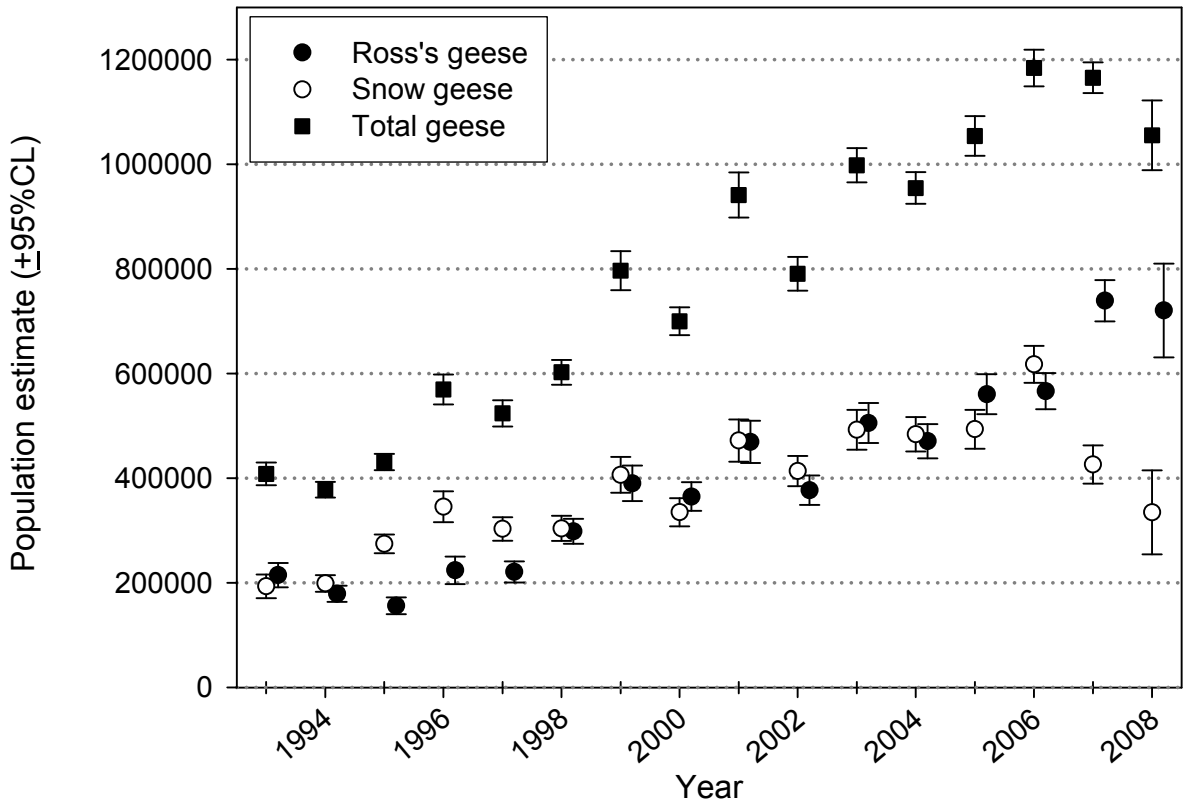


Figure 2.2. Post stratified sampling estimates of population size for Ross's and snow geese nesting at the Karrak Lake light goose colony, south of Queen Maud Gulf, Nunavut, Canada, 1993 to 2008.

3. ADULT BODY SIZE AND SPRING NUTRIENT RESERVES IN CONGENERIC ARCTIC GEESE OF DIFFERENT BODY SIZE

3.1 INTRODUCTION

Annual cycles of long-lived organisms are characterized by intermittent periods of high and low energy demands, corresponding to growth, migration or reproduction (Cooch et al. 1991a, Alisauskas 2002, Prop 2004). Consequently, the importance of nutrient supply changes throughout the annual cycle of an organism (Prop 2004). Failure to meet nutrient requirements of high-demand activities can influence fitness (Ankney and MacInnes 1978). In most species of waterfowl, endogenous nutrients are used to satisfy nutritional demands of migration and reproduction, when ambient food resources may fail to do so (Drent and Daan 1980, Alisauskas and Ankney 1992). For example, endogenous nutrient stores of arctic-breeding geese can significantly influence clutch size (Ryder 1970, Ankney and MacInnes 1978, Sedinger et al. 1995, Bon 1997, but see Choinière and Gauthier 1995) and are important for meeting metabolic demands of incubation when local foods are unavailable (Ankney and MacInnes 1978, Choinière and Gauthier 1995, Gloutney et al. 2001). Ultimately, annual variation in levels of pre-breeding nutrient reserves can influence production of young and thus, population dynamics (Alisauskas 2002).

It is well recognized that timing of reproduction by arctic-breeding geese is of paramount importance to their reproductive success (Ankney and MacInnes 1978, Cooke et al. 1984, Bêty et al. 2003). Delays in breeding due to severe arctic springs can significantly reduce clutch size and impinge on nesting success because, in the absence of food, geese must rely on, and can deplete, reserves to satisfy energy metabolism while waiting for snow to melt before nesting (Ryder 1970, Ankney and MacInnes 1978, Ankney 1984). However, structural size of females has the potential to influence fitness because body size limits the amount of nutrient reserve that an individual can transport to the breeding grounds (Ankney and MacInnes 1978). For example, in arctic-breeding geese, body size and clutch size were positively related (Alisauskas and Ankney 1990, but see Cooch et al. 1992). Larsson et al. (1998) found that structurally larger female barnacle geese (*Branta leucopsis*) produced larger clutches and eggs, hatched broods earlier, and produced more and heavier offspring than smaller females (Cooch et al. 1991a, Blanckenhorn

2000). Consequently, systemic decreases in body size may act to decrease reproductive output because it leads to an absolute reduction in the capacity to carry nutrient reserve. Still, the ability to achieve that capacity may also be limited by access to high quality foods for conversion to nutrient reserves during spring migration. Food acquisition may be hindered by snow cover but also by competition for foods on staging areas (Newton 2006). A decline in per-capita availability of foods on staging areas, stemming from increased density of geese, or long-term reduction of foods due to persistent grazing, may ultimately be a multifactorial combination of the number of conspecific and heterospecific geese, and their age, dominance, group size, and body size (Gawlik and Slack 1996, Newton 2006).

Populations of arctic-breeding geese have increased dramatically in recent years (Boyd et al. 1982, Ankney 1996, Alisauskas et al. 2009). Consequently, large increases in size of several populations of North American geese have resulted in ecosystem-level increases in arctic herbivory (Batt 1997). Particularly, declines in quality and quantity of food resources at some colonies have led to decreased growth and survival of offspring as well as adult body size (Cooch et al. 1991b, Cooch et al. 2002). Density-dependent competition for food could contribute to population regulation by decreasing productivity and survival (Sinclair 1989).

Two species of geese that nest sympatrically within the Queen Maud Gulf in Canada's central arctic have shown different population trajectories. Numbers of nesting lesser snow geese (*Chen caerulescens caerulescens*, hereafter snow geese) grew at an apparent annual rate of 16.7% from 1967 to 1988, while numbers of smaller-bodied Ross's goose (*Chen rossii*) nesters grew at only 7.9% per year during the same time period (Kerbes 1994). Since then, number of Ross's geese attempting to nest have grown at 11.0% per year, a rate roughly double that shown by sympatric nesting snow geese (Alisauskas et al. 2011a). This difference in population growth may have resulted from interspecific differences in immigration and emigration, and variation in annual survival of adults or interspecific variation in local production of young and subsequent recruitment. Life history theory predicts that populations under nutritional stress generally respond by decreasing juvenile survival, then by increasing age of maturity, and finally through depressing adult female reproductive rates (Eberhardt 2002). Age ratios (young/adults) of geese harvested by hunters can be used as an index of recruitment after adjusting for any age-related differences in vulnerability, and such age ratios are about twice as high for Ross's geese as are those for snow geese (Moser and Duncan 2001). In conjunction with equal relative vulnerability

of young to harvest between species (Chapter 6), this suggests that Ross's geese tend to have considerably higher recruitment than do snow geese. As part of an effort to begin to understand differences in population trajectory, I set out to study the effect of adult body size and spring nutritional condition on differences in recruitment. My first objective was to assess whether there has been a long-term decline in adult body size through time (1991 to 2008) in Ross's and snow geese. My second objective was to assess long-term (1993 to 2008) changes in stored nutrient reserves (fat and protein) of female geese of both species arriving to breed at Karrak Lake and examine the importance of year, population size, timing of reproduction, spring weather, and the spring conservation hunt to nutrient reserves.

The Ross's goose is the smallest of the North American light geese and is considered a smaller form of the snow goose (66% size of) because there are few morphological or genetic differences between the two (Anderson et al. 1992, Avise et al. 1992). Ross's geese may be closer to the minimum viable size for avian herbivores (Sedinger et al. 1998), and thus may show less plasticity in growth that poor forage conditions may influence in larger species. Density dependence on final adult body size is likely more severe in larger species because of increased costs of a longer developmental time and fast growth and/or starvation due to higher energy requirements than in smaller species (Blanckenhorn 2000). In this study, I assume Ross's and snow geese have similarly experienced recent changes in vegetation and associated nutrient availability for growing goslings, such as declines in highly digestible and nitrogen-rich foods (Slattery 2000); hence any changes in body size through time have likely been due to factors inherently associated with the major interspecific difference in body size. Consequently, I predicted that adult body size of snow geese would have decreased through time with no change in that of Ross's geese. Because of the reduction in snow goose recruitment and the importance of endogenous reserves to breeding, I predicted that there were simultaneous declines in absolute amounts of nutrients reserves (i.e., abdominal fat and muscle mass) of female geese arriving to nest at Karrak Lake. I also predicted that these declines should have been greater for snow geese than for Ross's geese. I suspect that more rapid declines in body size and concomitant changes in nutrient reserves of snow geese than of Ross's geese may have suppressed production of young snow geese, and thus their local population growth.

3.2 METHODS

3.2.1 Sample collection

In early-June of each year, I sampled adult female and accompanying male Ross's and snow geese (~25 of each species) with a shotgun as they arrived to nest. Geese were generally sampled over a seven day period during arrival. Because of differences in arrival phenology, snow geese were collected first with Ross's goose collections beginning a few days later (i.e., their respective seven day collection periods overlapped). Compared to accompanying males, females were identified by a more rounded abdominal profile due to the presence of rapidly developing ovarian follicles or oviducal eggs; only five of 845 sampled adult female geese did not show ovarian development (i.e., no developing follicles). Immature geese, which were identified by plumage characteristics, were not included in analyses (Ryder and Alisauskas 1995, Mowbray et al. 2000). I assumed sampled birds had recently arrived on the breeding grounds because I only targeted birds flying from the southwest (general direction birds travel from to reach colony), and birds already at the colony are generally confined to their nesting territory (Ryder and Alisauskas 1995). At base camp, birds were weighed (± 1.0 g) with a digital scale and measured (±0.1 mm) with dial calipers or ruler (head length, tarsus, and wing chord) (Alisauskas 2002). Birds were then dissected and organ and muscle masses were weighed (±0.1 g). I removed and emptied the gastro-intestinal tract (esophagus, gizzard, small intestine, large intestine, and caeca) to record total ingesta mass (Alisauskas 2002). Mass of reproductive tissues (ovary and oviduct) and numbers of developing follicles and post ovulatory follicles of each female were also recorded. I used the mass of one breast muscle and one bone-free leg muscle as an index of body protein (Alisauskas 2002), and the mass of abdominal fat was used as an index of fat reserve (Thomas et al. 1983).

3.2.2 Statistical analysis: Body size

I used principal component analysis (PCA, Proc PRINCOMP: SAS Institute v 9.1) from the correlation matrix of tarsus, head length, and wing chord to obtain principle component one (PC1) which provided a univariate index of body size. Species and sexes were pooled in the analysis to index size on the same scale. From 1991 to 2008 there were 498 Ross's and 571 snow geese with complete measurement data. There were no male geese sampled in 1993, 1999, and in 2000; male Ross's geese were also not sampled in 1992. Loadings of original variables on PC1

were 0.57, 0.58, and 0.57 for tarsus, head length, and wing chord, respectively; PC1 accounted for 90% of variation in all variables. Observed eigenvalues of PC1 scores were greater than expected according to broken stick criteria; PC1 was retained as my index of body size (McGarigal et al. 2000).

3.2.3 Statistical analysis: Body Condition

My analysis of body condition was limited to females only. Abdominal fat and protein reserve data were available for 16 years (1993-2008). I used a PCA, separate from above, from the correlation matrix of the tarsus, head length, and wing chord to obtain a univariate index of body size for each species separately because some variation in body condition can be explained by structural size (Ankney and MacInnes 1978). From 1993 to 2008 there were 735 female geese with complete measurement data; 394 snow geese and 341 Ross's geese. Loadings of original variables on PC1 were 0.57, 0.61, and 0.54 for Ross's geese and 0.60, 0.63, and 0.49 for snow geese, respectively. PC1 accounted for 54% and 53% of variation in all variables in Ross's and snow geese, respectively. PC1 (SIZE) was used in models as a covariate to control for size variation in fat and protein reserves (Mason et al. 2007). I tested whether somatic reserves of female geese that arrived to nest was also related to their potential clutch size, since individuals with more reserves lay larger clutch sizes (Ankney and MacInnes 1978, Bon 1997). Thus, I calculated the *apparent clutch size* (CS) of female geese by summing the number of developing and post ovulatory follicles. I used apparent clutch size as a continuous variable in models to control for nutrient reserve variation among arriving individuals. Breeding female geese also arrive at different stages of ovarian development. To account for variation in the investment of fat reserves into reproductive fat (RFAT) I calculated

Reproductive fat = [ovary mass * proportion fat (yolk)] + [number of post ovulatory follicles * (g fat/egg)];

As a measure of protein supplied to the reproductive protein (RPROT) I calculated

Reproductive protein = [ovary mass * proportion protein (yolk)] + [number of post ovulatory follicles * (g protein/egg)] + oviduct mass.

Fat and protein values for yolk and eggs were from Slattery and Alisauskas (1995). Additionally, I considered percent of apparent clutch size allocated (PCTALLOC) at arrival as a continuous covariate; I used the quotient of post ovulatory follicles over apparent clutch size (i.e.,

developing follicles + post ovulatory follicles). Arriving birds typically have postovulatory follicles because rapid follicle development is initiated before arrival onto breeding colonies resulting in 'dump' eggs during spring migration or on the colony (Raveling 1978, Bon 1997, Mowbray et al. 2000). Finally, I considered mass of the small intestine (SMINTWF) as a proxy for food ingested on penultimate staging areas before arrival onto the breeding colony. Because there is little or no food in much of the colony (Gloutney et al. 2001, Alisauskas et al. 2006a), food in gastro-intestinal tracts (INGESTA) of arriving geese provide a measure food intake before arrival onto the colony (Ankney 1977, Alisauskas unpubl. data). The SMINTWF was highly correlated with INGESTA ($r = 0.91$), so I used SMINTWF because INGESTA was not determined for all sampled geese among years.

3.2.4 Environmental Covariates

Spring weather. - Severe arctic springs (low temperatures and deep snow that can result in persistent snow cover on the breeding colony) reduce the number of young produced at the population level of midcontinent snow geese (Alisauskas 2002) probably because of reduced breeding propensity (Prop and de Vries 1993, Reed et al. 2004, Sedinger et al. 2006). Moreover, severe springs can inhibit access to food plants, cause delays in migration, and increase energy expenditure predictably reducing female body condition (MacInnes and Dunn 1988, Petersen 1992, Gauthier 1993). Such delays may result in nonrandom breeding effort with respect to body size, as smaller individuals refrain from attempting to nest in years of diminished nutrient reserves due to (1) incomplete storage, or (2) prenesting use of reserves during nesting delays.

I used weather data from the 3 nearest communities: Cambridge Bay (69˚ 06′ N, 105˚ 08′ W), Baker Lake (64˚ 18′ N, 95˚ 04′ W), and Gjoa Haven (68˚ 38′ N, 95˚ 51′ W) to create a spring severity index. June temperatures were averaged across the stations and May and June snow depths were summed separately across the stations (following Alisauskas 2002). Because there was no snow at any of the stations at the end of June I used snow depth for early-June (up to June 7). I believe that this approach permitted valid inference to be drawn about the relationship between body size, condition, and spring severity at latitudes that arriving geese likely experienced on their northward migration. I used mean June temperature, total May snow depth, and early-June snow depth in a PCA to construct a spring severity index. PCA of the correlation matrix resulted in PC1 with loadings of -0.48, 0.60, and 0.63; PC1 accounted for 69% of the

summed variance of the three variables. Thus, PC1 was used as an index of spring weather severity (SEVERITY) and positive PC1 values corresponded to lower mean June temperatures and deeper snow cover in late-May and early-June.

Timing of reproduction. - Seasonal delays in nesting reduce body condition of breeding geese (Barry 1962, Prop and de Vries 1993). Timing of nest initiation is governed by the disappearance of snow and exposure of nesting habitat; usually "late" years result when snow melt is delayed. I used mean nest initiation date (NID) calculated for each species as an index for timing of annual reproduction; NID for each species was used to model timing of reproduction for each year. Initiation date of nests located during egg-laying, was calculated by subtracting the number of eggs in the nest, less one, from the date of discovery. NID of nests found during incubation was obtained by subtracting stage of embryonic development (Weller 1956) and clutch size (assuming inter-egg intervals = 1.2 d for Ross's geese and 1.4 d for snow geese; Ryder and Alisauskas 1995, Mowbray et al. 2002) from the day the nest was found.

Population size.- Increasing numbers of arctic-breeding geese have amplified annual herbivory on northern staging areas causing severe cumulative damage on food plants (Abraham and Jefferies 1997, Jefferies et al. 2004). I used population size of the breeding colony in the current year as a proxy for density of geese on staging areas south of the breeding colony because annual increases in breeding populations of geese have predictably reduced carrying capacity of northern staging areas over time (Cooch et al. 1989). Population size, in a given year, was calculated based on stratified sampling using sample plots placed throughout the breeding colony on a 0.5 km grid system in areas of high density and a 1 km grid system in areas of low density (Alisauskas et al. 2011a). The total numbers of nests per plot were counted (see Alisauskas and Rockwell 2001). Population size of this colony has generally displayed a linear increase through time (Fig. 2.2). I used the quotient of population size in a given year divided by the smallest population size (377,956 geese) as a measure of relative size in my models; thus relative population size (POP) ranged from 1.0 to 3.13.

3.2.5 Parameter estimation and model selection

I developed candidate sets of models using general linear modeling (Proc GLM, SAS Institute v9.2) with the ESTIMATE option for parameter estimation. To examine variation in adult body size (PC1), I included SPECIES, SEX, YEAR, and SEVERITY as covariates in my candidate

model set. I considered YEAR as a linear trend (continuous variable) through time specifically to test whether body size showed a unidirectional trend over time as such changes in parameters may be density-dependent when simultaneous with increasing population size. I also included SEVERITY to account for possible annual variation in body size because I predicted that delayed breeding due to cold, springs with deep snow may skew the breeding cohort to be larger in body size than nonbreeders. I did not include NID in models of adult body size because I believed severe spring weather encountered during northern migration to be the proximate mechanism influencing body size in any given year (Sedinger et al. 2006). Likewise, I did not include POP in the current year as a measure of density dependence in my models because final adult body size is reached before age of sexual maturity and my sample included breeding adults of unknown age. I included a SEX effect in my models because male and female body size may have responded differently to density-dependent effects. For example, male snow goose goslings are predisposed to grow faster and larger than females. Thus, males should be more sensitive to periods of food restrictions and may be more apt to show declines in adult body size (Cooch et al. 1997). Finally, I considered interaction (*) effects among SPECIES*YEAR, SEX*YEAR, SPECIES*SEX, SPECIES*SEVERITY, and SEX*SEVERITY. I derived a suite of 25 *a priori* candidate models, and used an intercept-only model as my null model.

Model selection was then done to examine variation in protein and abdominal fat reserves of breeding female geese arriving onto the colony. To examine whether any changes in nutritional condition of arrivals was consistent with density dependence, I first modeled nutrient reserves as a linear trend through time (YEAR) with predictions of declines. I then considered models with POP as a proxy of density dependence because larger breeding populations of geese conceivably increase competition of food resources on northern staging areas. I acknowledge that POP and YEAR are redundant variables; I believe POP to be the mechanism for density dependence, while support for a declining YEAR trend could indirectly suggest density dependence. Finally, I considered models that included the spring conservation hunt (categorical variable; HUNT) to compare differences in abdominal fat and protein reserves between years with no hunt (1993 to 1998) and a hunt (1999 to 2008). Fèret et al. (2003) suggested that this conservation measure reduced spring body condition in greater snow geese (*Chen caerulescens atlantica*). These variables (YEAR, POP, and HUNT) were all highly correlated (r's $\geq$ 0.79), so each was considered alone in separate models. I constructed three global models (YEAR, POP,

and HUNT) for each nutrient reserve (e.g., SPECIES, SIZE, JULIAN (see below), CS, SMINTWF, RPROT (protein models only), RFAT (fat models only), NID, SEVERITY, YEAR, SPECIES*JULIAN, SPECIES*CS, SPECIES*RPROT, SPECIES*RFAT SPECIES*NID, SPECIES*SEVERITY, SPECIES*YEAR) and then considered progressively less complex models for each set. I included CS because I predicted that it should be related positively with nutrient reserves (Ankney and MacInnes 1978); specifically, although reserves should have a negative trajectory with increased allocation to reproduction, intercepts of these trajectories should be positively related to CS (Sedinger et al. 1997). I included collection date (DATE, julian date; continuous variable) of each bird in models to account for the possibility that individual quality of birds changes with time since arrival and calendar date (Alisauskas 2002). I also included a metric of proportional reproductive investment in models to account for variation in nutrient reserves resulting from allocation toward reproductive organ development and eggs of arriving birds; in some models I replaced total reproductive investment (RPROT or RFAT) with proportional reproductive investment by substituting PCTALLOC (see above). SEVERITY was included in models to estimate effects of cool springs with persistent snow cover on condition of arriving female geese. To further account for potential variation in nutrient reserves due to nesting delays, I also considered NID because individuals can deplete nutrient reserves in later years. I derived a limited set of 39 *a priori* candidate models for each analysis (i.e., protein and abdominal fat). I used an intercept only model as my null model.

The most plausible model was selected based on Akaike's Information Criterion (AIC_c) corrected for small sample size (Burnham and Anderson 2002). I used model weight (w_i) to evaluate likelihood of each model; w_i are normalized Akaike weights and indicate the relative support for different models in the candidate set, and can be interpreted as the evidence that a model is the most plausible, given the data and model set (Burnham and Anderson 2002). I summed w_i of all models (i.e., $\Sigma\, w_i$) with a given covariate and used this as a metric to assess importance (Burnham and Anderson 2002). I considered models $\leq 2\ \Delta\ AIC_c$ units to be of similar quality. I generated model-averaged estimates of parameters and unconditional standard errors from a confidence set of models, from which the evidence ratio was ≥ 0.125, if model uncertainty was present (Burnham and Anderson 2002).

3.3 RESULTS

3.3.1 Body size

Overall, there appeared to be significant annual variation in mean estimates of body size (Fig. 3.1). Notably, the best approximating model for explaining variation in body size of Ross's and snow geese included additive effects of SPECIES, SEX, and SEVERITY; it had a model weight, $w_i = 0.33$ (Table 3.1, Model {1}). This model suggested that size of adults showed consistent differences among species and sexes, though this changed with the relative severity of spring weather. The second best model ($w_i = 0.25$, $\Delta AIC_c = 0.52$) was similar to the top ranked model but included an additive effect of YEAR and interactive effects of SPECIES*SEX and SEX*YEAR (Table 3.1, Model {2}). Another competing model ($w_i = 0.13$, $\Delta AIC_c = 1.78$) was similar to the top ranked model but included an additive effect of YEAR (Table 3.1, Model {3}). All other models had Akaike weights, $w_i \leq 0.10$, and $\Delta AIC_c \geq 2.40$) and so had less support relative to the three best models.

There was strong evidence that body size of sampled geese increased with spring severity ($\overline{\hat{\beta}}_{severity} = 0.06$, 95% CL: 0.03, 0.08; $\Sigma w_i = 1.00$). Although species (Ross's coded as a '1' and snow coded as a '0' in the design matrix) ($\overline{\hat{\beta}}_{species(ross)} = -3.13$, 95% CL: -3.30, -2.96; $\Sigma w_i = 1.00$) and sex effects were expected ($\overline{\hat{\beta}}_{female(snow)} = -0.78$, 95% CL: -1.00, -0.56; $\Sigma w_i = 1.00$), there was evidence of a SPECIES*SEX interaction ($\overline{\hat{\beta}}_{species*sex(ross)} = 0.18$, 95% CL: 0.03, 0.32; $\Sigma w_i = 0.44$) showing that female Ross's geese were of more similar body size to male Ross's geese ($\overline{\hat{\beta}}_{female(ross)} = -0.60$, 95% CL: -0.82, -0.33) than were female snow geese to male snow geese. Overall, I found inconclusive evidence that geese had declined in size through time ($\overline{\hat{\beta}}_{year(males)} = 0.015$, 95% CL: -0.01, 0.03; $\Sigma w_i = 0.60$). However, there was some evidence for a SEX*YEAR interaction ($\overline{\hat{\beta}}_{sex*year(female)} = -0.02$, 95% CL: -0.04, -0.01; $\Sigma w_i = 0.47$), which suggested that female geese of both species declined in structural size through time ($\overline{\hat{\beta}}_{year(females)} = -0.007$, 95% CL: -0.01, 0.01), although the 95% CL included zero. Finally, there was virtually no support for variation in body size in relation to a SPECIES*YEAR interaction ($\overline{\hat{\beta}}_{species*year} = 0.002$, 95% CL: -0.01, 0.01; $\Sigma w_i = 0.04$), a SPECIES*SEVERITY interaction ($\overline{\hat{\beta}}_{species*severity} = -0.01$, 95% CL: -

0.06, 0.03; $\Sigma w_i = 0.05$) or a SEX*SEVERITY interaction ($\overline{\hat{\beta}}_{sex*severity} = -0.02$, 95% CL: -0.08, 0.03; $\Sigma w_i = 0.06$).

3.3.2 Body condition: protein and abdominal fat

Annual mean values of protein reserves suggested that females' of both species displayed decreases through time (Fig. 3.2). I initially considered 39 models as the candidate set for protein reserves. However, after assessing estimates of protein reserves it became apparent that the data approximated a quadratic trend. Consequently, I considered an additional seven *a posteriori* models with quadratic effects of population size (POP^2) and year ($YEAR^2$); these models were best supported by the data (Table 3.2). The most plausible model included additive effects of SPECIES, SIZE, DATE, PCTALLOC, CS, POP, and POP^2; with interaction effects of SPECIES*POP and SPECIES*POP^2. The second-ranked model was similar to the best approximating model but included an additive effect of NID (Table 3.2, Model {2}, $w_i = 0.34$, $\Delta AIC_c = 1.29$). All other models had Akaike weights, $w_i \leq 0.02$, and $\Delta AIC_c \geq 7.18$, and so had virtually no support relative to the top two models (Table 3.2).

Overall, modelling results suggested that absolute protein reserves were smaller in Ross's geese (coded as '1' in design matrix) than in snow geese (coded as '0'; $\overline{\hat{\beta}}_{species(ross)} = -81.77$, 95% CL: -118.60, -44.98; $\Sigma w_i = 1.00$), but this was expected because of the size disparity between the species. With respect to intraspecific variation in body size, larger geese had greater protein reserves than did smaller ones ($\overline{\hat{\beta}}_{size} = 8.36$, 95% CL: 7.08, 9.64; $\Sigma w_i = 1.00$). Similarly, individuals with larger apparent clutch sizes had greater protein reserves ($\overline{\hat{\beta}}_{CS} = 2.86$, 95% CL: 1.59, 4.14; $\Sigma w_i = 1.00$), although there was less protein if females had formed a greater proportion of their apparent clutch size ($\overline{\hat{\beta}}_{PCTALLOC} = -7.43$, 95% CL: -13.17, -1.69; $\Sigma w_i = 1.00$). Models with RPROT did not perform well possibly because range in total reproductive investment present in my sampled geese was limited to an abbreviated period early in the laying cycle that overlapped with arrival, and did not span the entire laying period which continued after bird arrived and began to construct nests. Finally, for every calendar day that geese were sampled after arrival onto the colony, they lost 0.7 g of protein reserve ($\overline{\hat{\beta}}_{date} = -0.71$, 95% CL: -1.38, -0.04; $\Sigma w_i = 0.98$) corrected for all other effects in the model.

There was substantial evidence for a curvilinear decline in protein reserves with increasing population size ($\overline{\hat{\beta}}_{pop(snow)}$ = 49.54, 95% CL: 24.81, 74.26; $\overline{\hat{\beta}}_{pop^2(snow)}$ = -16.51, 95% CL: -22.23, -10.78; Σw_i = 1.00), a pattern of decline consistent with increased competition of food resources on northern staging areas. However, a SPECIES* POP^2 interaction ($\overline{\hat{\beta}}_{species*pop(ross)}$ = -35.97, 95% CL: -72.18, 0.24; $\overline{\hat{\beta}}_{species*pop^2(ross)}$ = 11.96, 95% CL: 3.62, 20.29; Σw_i = 1.00) suggested that declines in Ross's geese were less severe than in snow geese ($\overline{\hat{\beta}}_{pop(ross)}$ = 13.56, 95% CL: -14.67, 41.79; $\overline{\hat{\beta}}_{pop^2(ross)}$ = -4.55, 95% CL: -11.02, 1.92) (Fig. 3.3). Delays in timing of breeding suggested that geese increased acquisition of protein, although the 95% CL of the estimated slope included zero ($\hat{\beta}_{NID}$ = 0.34, 95% CL: -0.43, 1.12; Σw_i = 0.36). Models that included quadratic effects of year were of low quality and low explanatory power ($\geq \Delta AIC_c$ = 14.70; Σw_i = 0.00). The best model that included a year effect {SPECIES, SIZE, DATE, CS, PCTALLOC, NID, YEAR, YEAR^2, SPECIES*YEAR, SPECIES*YEAR^2} predicted an increase then decline in snow goose protein reserves through time ($\hat{\beta}_{year(snow)}$ = 0.91, 95% CL: -1.32, 3.15; $\hat{\beta}_{year^2(snow)}$ = -0.27, 95% CL: -0.41, -0.14). However, a SPECIES*YEAR^2 interaction ($\hat{\beta}_{species*year(ross)}$ = -2.29, 95% CL: -5.64, -1.06; $\hat{\beta}_{species*year^2(ross)}$ = 0.27, 95% CL: 0.08, 0.47) suggested that the temporal pattern in Ross's geese was attenuated compared to snow geese ($\hat{\beta}_{year(ross)}$ = -1.38, 95% CL: -4.05, 1.29) ($\hat{\beta}_{year^2(ross)}$ = 0.00, 95% CL: -0.16, 0.16).

Finally, protein reserve models structured with the inclusion of conservation order hunt were of particularly low quality ($\geq \Delta AIC_c$ = 76.43; Σw_i = 0.00). In the top model for protein reserves that included HUNT {SPECIES, SIZE, DATE, CS, PCTALLOC, HUNT, NID, SEVERITY, SPECIES*HUNT}, snow geese collected before the conservation hunt (until 1998) had larger protein stores than in years with a hunt ($\hat{\beta}_{hunt(snow)}$ = 25.92, 95% CL: 20.38, 31.45). However, a significant SPECIES*HUNT interaction ($\hat{\beta}_{species*hunt(ross)}$ = -17.52, 95% CL: -25.21, -9.83) suggested a diminished effect of HUNT on protein reserves of Ross's geese ($\hat{\beta}_{hunt(ross)}$ = 8.40, 95% CL: 14.46, 2.33) with the implementation of the conservation hunt. Least-square means implied that Ross's geese showed smaller declines in protein reserves (No hunt = 185.0 g,

95% CL: 179.9, 190.0 g; hunt = 176.5 g, 95% CL: 173.5, 179.5 g; P = 0.007) than snow geese (No hunt = 292.9 g, 95% CL: 288.1, 297.8 g; hunt = 267.0 g, 95% CL: 264.3, 269.7 g; P < 0.0001) before and during the spring conservation hunt, respectively. HUNT was related to, and confounded with, YEAR and POP, so it was difficult to conclusively separate their effects on protein reserves. Although, CLs in parameter estimates relating protein reserves to the conservation hunt were largely different from zero, the apparent effect of HUNT was likely spurious. Model quality was superior if protein reserves were structured against POP rather than HUNT.

Annual mean abdominal fat values suggested that snow geese displayed larger decreases through time than Ross's geese (Fig. 3.4). The best approximating model considered for abdominal fat included additive effects of SPECIES, SIZE, CS, PCTALLOC, NID, and YEAR; with interaction effects of SPECIES*YEAR and SPECIES*CS (Table 3.3, Model {1}, w_i = 0.26). The second most probable model was similar in structure to the best model but included an effect of SEVERITY (Table 3.3, Model {2}, w_i = 0.17, ΔAIC_c = 0.86). Last, the third most likely model was analogous to the top-ranked model but included an effect of POP instead of YEAR (Table 3.3, Model {3}, w_i = 0.13, ΔAIC_c = 1.30). All other models had Akaike weights, $w_i \leq$ 0.07, and $\Delta AIC_c \geq 2.47$) and so had less support relative to the top three models.

Based on the large difference in structural size between species, abdominal fat reserves were predictably smaller in Ross's geese than in snow geese ($\bar{\hat{\beta}}_{species(ross)}$ = -22.83, 95% CL: -38.98, -6.67; Σw_i = 1.00). With respect to intraspecific variation in body size, larger individuals carried greater fat stores than did individuals of smaller size ($\bar{\hat{\beta}}_{size}$ = 3.41, 95% CL: 2.36, 4.47; Σw_i = 1.00), suggesting a structural limit to how much fat they could carry. Likewise, individuals with larger apparent clutch sizes had larger fat reserves ($\bar{\hat{\beta}}_{CS(snow)}$ = 4.01 g/egg, 95% CL: 2.67, 5.36; Σw_i = 1.00). However, a SPECIES*CS interaction ($\bar{\hat{\beta}}_{species*CS(ross)}$ = -2.87 g/egg, 95% CL: -4.99, -0.74; Σw_i = 0.91) suggested that the slope of the relationship between fat reserves and CS in snow geese was more than the slope in Ross's geese ($\bar{\hat{\beta}}_{CS(ross)}$ = 1.15 g/egg, 95% CL: -0.53, 2.83), partly because their Ross's goose eggs contain less fat than snow goose eggs. Moreover, individuals that were sampled with a greater proportion of their clutch already formed had significantly less fat in reserve ($\bar{\hat{\beta}}_{PCTALLOC}$ = -10.60, 95% CL: -15.32, -5.88; Σw_i = 1.00). A model

that included RFAT was of substantially lower quality ($\Delta AIC_c = 30.62$). Models with RFAT did not perform well (see above).

Overall, there was a significant linear decline in fat reserves of snow geese from 1993 to 2008 ($\bar{\hat{\beta}}_{year(snow)} = -1.48$ g/year, 95% CL: -1.97, -1.00; $\Sigma w_i = 0.62$), consistent with density dependence. The difference in slopes between snow and Ross's geese ($\bar{\hat{\beta}}_{species*year(ross)} = 1.73$, 95% CL: 1.05, 2.41; $\Sigma w_i = 0.62$) suggested that snow geese incurred greater effects of density dependence compared to Ross's geese ($\bar{\hat{\beta}}_{year(ross)} = 0.25$, 95% CL: -0.31, 0.80) (Fig. 3.5a). There was also strong evidence that fat reserves declined predictably with delays in breeding by both species ($\bar{\hat{\beta}}_{NID} = -2.20$, 95% CL: -2.67, -1.74; $\Sigma w_i = 1.00$) (Fig. 3.5b). Models without NID generally did not perform well; a model structure similar to the top model, but excluding NID {SPECIES, SIZE, CS, PCTALLOC, YEAR, SPECIES*CS, SPECIES*YEAR}, was of substantially lower quality ($\Delta AIC_c = 135.21$). Spring severity was not as important as timing of breeding, even though the two effects were correlated ($r = 0.57$), but there was some support for an effect of SEVERITY on fat reserves by snow geese ($\bar{\hat{\beta}}_{severity(snow)} = -1.47$, 95% CL: -3.05, 0.12; $\Sigma w_i = 0.48$) and some evidence from a SPECIES*SEVERITY interaction ($\bar{\hat{\beta}}_{species*severity(ross)} = 1.84$, 95% CL: -0.19, 3.88; $\Sigma w_i = 0.18$) suggesting that Ross's geese experienced smaller effects of spring severity on fat reserves than snow geese ($\bar{\hat{\beta}}_{severity(ross)} = 0.38$, 95% CL: -1.38, 2.13), though estimates were imprecise. Effects of population size, as a proxy of increased food competition on staging areas, were less supported than a linear decline over the course of the study. Still, there was some evidence of differential responses between species fat reserves with increasing population size ($\bar{\hat{\beta}}_{species*pop(ross)} = 10.16$, 95% CL: 5.97, 14.37; $\Sigma w_i = 0.37$). Snow geese experienced reductions in fat reserves with increasing population size ($\bar{\hat{\beta}}_{pop(snow)} = -8.92$, 95% CL: -11.82, -6.03), while Ross's geese did not ($\bar{\hat{\beta}}_{pop(ross)} = 1.24$, 95% CL: -2.00, 4.47).

Finally, although models that included effects of HUNT were of low quality ($\geq \Delta AIC_c = 22.86$; $\Sigma w_i = 0.00$), the effect was accurately estimated allowing interpretation of the spring conservation hunt on abdominal fat storage. The best model which included HUNT {SPECIES, SIZE, JULIAN, CS, PCTALLOC, HUNT, NID, SPECIES*CS, SPECIES*HUNT} suggested

disparate responses between species in relation to the initiation of the spring conservation hunt ($\hat{\beta}_{species*hunt(ross)}$ = -14.59, 95% CL: -20.94, -8.24). Snow geese collected during the period preceding efforts to reduce population size (until 1998) had larger abdominal fat stores than during efforts of population reduction (after 1998) ($\hat{\beta}_{hunt(snow)}$ = 9.38, 95% CL: 4.87, 13.89), while fat reserves of Ross's geese ($\hat{\beta}_{hunt(ross)}$ = -5.21, 95% CL: -10.13, -0.29) displayed a trend contrary to the predicted effect. Least-square means showed that Ross's geese slightly increased abdominal fat reserves (No hunt = 54.5 g, 95% CL: 50.5, 58.6 g; hunt = 59.6 g, 95% CL: 57.1, 62.0 g; P = 0.04), while snow geese displayed significant declines in fat reserves in response to the spring hunt (No hunt = 81.8 g, 95% CL: 77.9, 85.8 g; hunt = 72.8 g, 95% CL: 70.7, 74.9 g; P < 0.0001).

3.3.3 Delayed nesting phenology

Because of large long-term reductions in spring nutrient reserves, I performed an *ad hoc* analysis to examine if nest initiation dates have changed through time. I predicted that geese may be arriving later to breed because more time may be necessary to acquire or prospect food sources to satisfy nutritional demands of migration and/or reproduction. To examine changes in timing of breeding, I used nest initiation dates from 11,942 Ross's goose nests and 11,417 snow goose nests found at the Karrak Lake colony during 1991 to 2008. I used the mean nest initiation date calculated for each species separately per year to create an early-late index (ELI) of timing of nesting. The ELI was calculated as the difference between the annual mean and the long-term average nest initiation for 1991-2008. I believed that timing of nest initiation is governed largely by the disappearance of snow and exposure of nesting habitat (SEVERITY); usually "late" years result when snow melt is delayed. I performed simple linear regression of ELI on SEVERITY for each species separately and used residuals as a delay index. I then performed simple linear regression of the delay index on YEAR to examine if birds were breeding later. Results suggested that Ross's (F = 4500.99, df = 1 and 11940, r^2 = 0.27, P < 0.0001; slope = 0.36, 95% CL: 0.35 to 0.37) and snow geese (F = 2289.39, df = 1 and 11416, r^2 = 0.17, P < 0.0001; slope = 0.28, 95% CL: 0.27 to 0.30) have attempted to nest later, more recently, than they had at the start of my study. Thus, over the 18 years of study Ross's and snow geese are now breeding 6.5 and 5.0 days later, respectively.

3.4 DISCUSSION

3.4.1 Body size

There were no large, long-term declines in body size of male geese that accompanied females arriving to nest at Karrak Lake, regardless of species. Such declines are predictable if there is severe density-dependence on the ability of goslings to feed and grow properly. Declines in time series of body size for adults sampled from superpopulations (Reed and Plante 1997, Loonen et al. 1997, Alisauskas 2002) have been associated with concurrent local declines in per capita food availability detected at specific brood-rearing areas, the period after which juvenile geese experience little compensatory growth (Cooch et al. 1991b, Sedinger 1992, Lindström 1999). Further, because goslings of arctic-breeding geese exhibit some of the most rapid rates of growth among precocial birds (Whitehead et al. 1990), morphological selection could occur with severe resource limitation. I predicted that the larger-bodied snow goose would experience greater reductions in size because of their absolutely higher nutritional demands and longer development time as goslings compared to Ross's geese (MacInnes et al. 1989). In previous studies conducted at specific breeding areas, snow geese had shown temporal decreases in body size as the size of local nesting populations grew, while black brant (*Branta bernicula nigricans*), a small-bodied species had not (Cooch 1991b, Sedinger et al. 1998). Goslings of small goose species may be better adapted to attenuate effects of diminished feeding conditions on their growth and final size because they have better digestive efficiency (larger gizzards), locomotor capacity (step rates), and smaller bill morphology which allow for better assimilation of nutrients in comparison to larger species (Slattery and Alisauskas 1995, Ankney 1996, Pezzanite 2003).

I believed that reductions in snow goose size would ultimately reduce their fecundity because the two are interconnected, and environmentally induced phenotypic change can have major fitness consequences (Larsson and Forslund 1991, Alisauskas and Ankney 1990, Sedinger et al. 1995, Larsson et al. 1998, Blanckenhorn 2000, but see Cooke et al. 1995). However, my sample of geese was limited to prospective breeders arriving to the nesting colony; non-breeding geese form large flocks outside of the colony boundary (Alisauskas, personal obs.) and were not sampled judging from the absence of birds with undeveloped reproductive organs in my sample. If size influenced breeding probability, I may have only collected larger birds. For example, Sedinger et al. (1995) showed that smaller geese had lower frequency of breeding, though in a

sub-arctic snow goose population Cooch et al. (1999) documented no difference in breeding occurrence among larger or small individuals. Notably, Slattery (2000) documented reductions in size of goslings reared in a biodeterioration zone around the Karrak Lake colony. Although I could not access nonbreeding birds to sample them outside of the colony concurrently with prospective breeders at the colony, nonbreeding birds may now form a larger proportion of the population than they had in the past. Alisauskas (2002) collected snow geese from the superpopulation during spring migration (April through May) through agricultural lands in Manitoba, Canada, before departure to breeding areas; he documented a long-term decrease in body size of both male and female geese, although he was unable to stratify the sample by likelihood of breeding.

Male goslings are predisposed to grow faster and larger than females such that males are more sensitive to periods of food restrictions (Clutton-Brock et al. 1985, Cooch et al. 1997). Consequently, males should show declines in adult body size (Cooch et al. 1997). Thus, although I predicted that density-dependent effects would be stronger on male geese compared to females at Karrak Lake, there was some evidence to suggest that female geese displayed a decreasing trend in structural size through time, while male geese did not. There may have been phenotypic selection against smaller males in relatively poor body condition through mortality during fall migration, with the result that larger males are recruited into the local population. If female geese preferentially pair with male geese from similar breeding areas and small male geese have increased rates of mortality, then perhaps this explains the observed trend (Choudbury and Black 1994). However, the apparent trend may also have resulted from higher philopatry to breeding areas by females than males (Drake and Alisauskas 2004); if food restrictions at Karrak Lake influenced adult body size, then females that have a higher likelihood of having been raised locally may have exhibited declines in body size while males may have had a higher likelihood of immigration from other colonies without density-dependent effects on body size where they were reared (Anderson et al. 1992, Larsson and Forslund 1992).

I found strong support for an additive effect of spring severity on body size of geese. Reed et al. (2004) surmised that spring snow cover and amount of stored endogenous reserves are important variables in arctic-goose breeding propensity. My results showed that, in years with colder temperatures and more snow, body size of both Ross's and snow geese sampled in the colony as prospective breeders was larger. By contrast, the reduction in size in years with

warmer temperatures and less snow may have improved breeding propensity of individuals of all sizes, but disproportionately so for smaller geese. Selection for larger size, within years of severe spring weather, is likely brought about by the ability of larger individuals to store absolutely more nutrient reserves required for clutch formation and incubation. More complex interactions with an interplay between body size, previous breeding experience, and breeding probability are also possible with events other than local variation in arctic climate. For example, Sedinger et al. (2006) found that breeding probability of inexperienced, younger black brant was reduced in El Niño years more so than in older, experienced individuals.

3.4.2 Body condition

Although I did not detect large density-dependent declines in body size as predicted, my results about spring nutrition of prospective breeders generally were consistent with density dependence. Cumulative damage of vegetation by geese of the kind documented by Alisauskas et al. (2006) within the nesting colony or by Slattery (2000) on local brood-rearing areas near Karrak Lake may also have occurred on sub-arctic and arctic habitats important for continued nutrient reserve storage before attempted breeding. Food acquisition along northern staging areas is important for reproduction, recrudescence of reproductive organs, and energy metabolism (Wypkema and Ankney 1979, Bon 1997). Mid-continent Ross's and snow geese are at their best body condition upon arrival onto breeding areas (Ankney and MacInnes 1978, Wypkema and Ankney 1979, Bon 1997). These geese store endogenous reserves during spring migration in two major episodes; nearly all fat reserves are obtained in prairie Canada, while protein reserves are acquired on northern staging areas (Wypkema and Ankney 1979, Alisauskas and Ankney 1992, Bon 1997). For instance, Wypkema and Ankney (1979) documented that female snow geese leaving a spring staging area maintained fat reserves, gained ~14 g protein (equivalent to the protein in one egg), and increased overall body mass 240 g; Bon (1997) documented similar trends for fat and protein reserves in Ross's geese. Moreover, these geese arrived with developing ova and initiated nests within 3 days after arrival and thus have little opportunity to compensate for reduced somatic stores or assimilate breeding colony forage into clutch formation (Ankney and MacInnes 1978, Gloutney et al. 2001, Chapter 3). Other species of arctic geese initiate rapid follicle growth, and feed up to 14 days after arrival onto nesting areas, may not experience similar decreases in reproductive output because they incorporate significant

amounts of breeding colony vegetation into clutch formation (Raveling 1978, Budeau et al. 1991, Choinière and Gauthier 1995). Yet, studies that examined the effect of the spring conservation hunt in greater snow geese (*Chen caerulescens atlantica*), a species with a long time lag between arrival in nest initiation, have documented significant decreases in body condition and reproductive output apparently from the disturbance to feeding associated with spring hunting on Canadian agricultural staging areas (Fèret et al. 2003, Mainguy et al. 2003).

I was unable to conclusively determine whether similar declines observed in snow goose nutrient reserves (and smaller declines in Ross's geese) at Karrak Lake following initiation of the conservation hunt in spring of 1999 were due, in fact, to the hunt or to simultaneous density dependence from rapid population growth. In either case, the predicted changes in Ross's geese were smaller than in snow geese. Differences in body size, metabolic rate and concurrent life history traits may be important factors that impinge on the importance of density dependence on spring nutrient storage. Because of their larger body size, snow geese require more time following hatch for complete development of goslings until they can attain flight. An adaptation for protracted residence in arctic areas by snow geese compared to Ross's geese is the earlier departure from the spring staging areas in prairie Canada (Dzubin 1965) and earlier arrival and breeding at arctic colonies (see above). During northward migration, robust bill morphology of snow geese allows foraging by grubbing roots and rhizomes before significant above-ground growth of vegetation (Ganter & Cooke 1996, Jefferies et al. 2004). Grubbing, which can weaken plants, has the potential to cause severe damage to swards and significant cumulative damage with large increases in annual population size (Kerbes et al. 1990, Jefferies et al. 2004, Alisauskas et al. 2006a). Thus, the rapid decrease in protein stores in snow geese has likely resulted from a large decrease in per capita forage availability. Arctic geese need to forage extensively on high quality foods, not only to provide energy metabolism for migration and reproduction, but to acquire proper nutrition since protein and metabolizable energy are relatively low in food plants (Sedinger 1984, Sedinger 1997). By contrast, Ross's geese delay northward migration and, their smaller bill morphology may allow grazing of newly emerging grasses, roots of sedges (Cyperaceae), and other vegetation on swards damaged by snow geese, thereby resulting in reduced impact on ability of Ross's geese to store protein compared to snow geese. Delayed arrival onto staging areas may also benefit their protein acquisition because intense grazing by vanguard snow geese may enhance productivity of forage plants on remnant

patches (Hik and Jefferies 1990). However, it is also conceivable that Ross's geese have affinities for different staging areas between the prairies and nesting colonies, although locations and extent of species overlap at such staging areas in boreal, taiga and arctic areas remain unknown, and is a topic in need of research.

Density dependence on staging areas may indirectly limit reproductive output by delaying timing of reproduction (Newton 2006). I documented that Ross's and snow geese are now breeding ~6.5 and 5.0 days later than would be expected from annual variation in spring severity, over the course of study. For example, anecdotal evidence in breeding season 2009, when conditions at the breeding colony were indicative of an early year (little snow, warmer temperatures), supported the conclusion that geese are nesting later at Karrak Lake because mean nest initiation dates were the latest recorded in 19 years of study (Alisauskas unpubl. data). I believe decreased food availability on staging areas cause geese to nest later since geese increasingly spend more time prospecting new sources of food (Newton 2006). Some recent studies on geese suggest that nutritional condition and food acquisition rate on staging areas can influence migration chronology (Drent et al. 2003). Prop et al. (2003) suggests that deteriorating forage conditions actually cause geese to migrate perhaps looking for new food sources, which may delay arrival and initiation of breeding. Further, in a study of migrating swans, those that arrived later on a staging area stayed longer refueling because of increased competition for available foods (Nolet and Drent 1998). Last, a large scale study on spring migrating lesser scaup (*Aythya affinis*), showed that females experienced declines in fat reserves over time with the potential to decrease breeding probability and/or delay nesting, both of which can lead to reductions in population growth (Anteau and Afton 2009).

Because body condition of individuals at time of breeding provides a measure of the ability of the individual to meet current energetic needs of metabolism and reproduction, decreases in condition directly reduce reproductive output. Significantly reduced spring nutrition of snow geese may impinge on reproductive output in two ways. First, diminished protein reserves may lead to reductions in breeding probability and clutch size. There is evidence that somatic protein reserves are related to clutch size in some arctic-breeding geese (Bon 1997, Croft 1999, this study). By contrast, decreases in fat reserves may act to decrease breeding propensity, clutch size, and the capacity to complete incubation. Initiation of rapid follicle development (breeding probability) in lesser scaup seems to be controlled by a nutrient-reserve threshold

(DeVink et al. 2008). Alisauskas (2002) specifically documented the importance of fat reserves to high production of goslings by snow geese at the population level. In geese, nest success may become compromised because increased feeding breaks reduce incubation constancy needed for developing embryos and increase predator exposure, while low fat reserves may render birds unable to fend off predators or cause nest abandonment (Thompson and Raveling 1987). Because snow geese build less insulated nests compared to Ross's geese and have a proclivity to nest on exposed rocky habitat, decreases in incubation constancy may impinge on embryo development and hatching (McCracken et al. 1997). The smaller body size of Ross's geese reduces absolute food requirements and, in conjunction with more-insulated nests, may reduce the degree to which food may be required during incubation breaks. Ross's geese construct larger and more insulated nests, which not only likely maintain adequate embryonic heat needed for development and hatching during incubation breaks (McCracken et al. 1997), but may reduce energy expenditure of incubating females compared to snow geese.

Competition for food is considered the major mechanism behind density dependence on reproductive output, although environmental conditions can also alter spring feeding conditions. My results suggest more annual variability in abdominal fat than protein stores. Delayed breeding stalls migrating geese on staging areas south of breeding colonies where they catabolize fat reserves (Barry 1962). Fat reserves serve as the primary energy source on northern staging areas when snow limits access to food plants while also providing energy required for flight time to new areas for food. Alisauskas (2002) noted the importance of factors, such as annual variation in agricultural food availability, weather, and migration chronology that influenced fat storage during spring migration through prairie Canada. However, results supported herein suggest delayed breeding due to density dependence on spring nutrition may be decreasing fat reserves. For instance, fat reserves in Ross's geese actually displayed a slight increasing trend through time, but a strong additive effect of timing of breeding suggested that geese lost 2.20 g fat/day. Thus if Ross's geese are breeding 6.5 d later then total fat loss due to delayed breeding may be 14.3 g. By contrast, in delayed years, geese may have more time to acquire protein from forage plants particularly if birds are migrating along the snow line where spring green-up occurs (Prop and Deerenberg 1991). Bauer et al. (2008) showed that Pink-footed geese (*Anser brachyrhynchus*) used local accumulated temperatures to increase their rate of their spring migration to colonies when it was warmer and subsequently predicted geese to skip their

northern most staging area during early springs to head for breeding colonies. This would suggest less opportunity to exploit green vegetation for protein acquisition in early years. However, there is also evidence that late springs (low temperatures and wet weather) increase food quality so that geese are more able to easily assimilate large amounts of protein (Prop and Deerenberg 1991, Langvatn et al. 1996, Ericsson et al. 2002). The optimal time to nest is likely a balance between the adaptiveness of nesting early through benefits to gosling survival (Chapter 6) and nesting late enough to permit proper storage of nutrients required for production of eggs and successful reproduction.

It seems unlikely that the spring conservation hunt has had a large impact on spring nutrition of mid-continent Ross's or snow geese nesting at Karrak Lake. The spring hunt was thought to reduce body condition and reproductive output in greater snow geese due to disturbance in feeding episodes as geese funnel through agricultural land in the St Lawrence River valley in southern Quebec. Fèret et al. (2003) documented a large reduction (29 to 48%) in abdominal fat and smaller decreases in breast protein (5 to 11%) due to the spring hunt. My results were similar in proportional protein reduction but abdominal fat decrease in my study was substantially less (9 to 12%). However, as noted in results, the declines in nutrient reserves were explained as well as or better by models consistent with density dependence (Cooch et al. 1991b), than with the presence of a conservation hunt.

In sum, this long-term study has documented reduced spring nutrition of Ross's and snow geese arriving to Karrak Lake as prospective breeders. To my knowledge, this is the first evidence demonstrated that is consistent with density dependence in spring goose nutrition on staging grounds. My interspecific comparison of these two closely-related, sympatric breeding species showed that larger-bodied snow geese experienced more rapid declines in fat and protein reserves. I believe that long-term declines in nutrient storage, concurrent with delayed timing in breeding (5 days), will exacerbate continued reproductive decline in snow geese. For example, these carry-over effects from spring migration could decrease breeding probability (i.e., decrease in numbers of snow goose breeding pairs since 2006; Fig. 2.2), clutch sizes, and nest success. I previously documented (Chapter 4) that snow geese relied on endogenous reserves for clutch formation and incubation once reaching the breeding colony in comparison to Ross's geese. Thus, demonstrated declines in clutch size and nest success (Chapter 5) should have greater effects on the relative production of goslings fledged per adult snow goose. Depending on

compensations in adult and juvenile survival, these reductions in gosling production by snow geese may be sufficiently lower than in Ross's geese to have different consequences in local population dynamics. Finally, because staging areas of migratory birds are of extreme importance (Newton 2006), this study underscores the need to locate northern staging areas of Ross's and snow geese nesting within the Queen Maud Gulf Migratory Bird Sanctuary. Although interplay of nutrient storage in agricultural landscapes (Bon 1997, Alisauskas 2002), and coastal Hudson Bay (Wypkema and Ankney 1979), with arctic climate (Alisauskas 2002, this chapter), has received attention, there is a need to better understand nutritional ecology of arctic-breeding geese in the boreal, taiga and tundra habitats of central Canada. Location of such staging areas, information about use and overlap of goose species, and the extent of damage to vegetation communities would be beneficial for understanding continental population dynamics, and may benefit management and conservation of these arctic-breeding geese.

Table 3.1. Top models for variation in body size of Ross's (n = 498) and snow (n = 571) geese arriving or breeding at the Karrak Lake light goose colony, south of Queen Maud Gulf, Nunavut, Canada, from 1991 to 2008. Only the top eight of twenty-five models in the candidate set are shown, ranked by ascending ΔAIC_c. All other models had ΔAIC_c >7.00.

Number/Model[a]	AIC_c[b]	ΔAIC_c[c]	w_i[d]	K[e]	SSE[f]	R^2[g]
1 {Species, Sex, Severity}	-1466.16	0.00	0.33	7	267.67	0.91
2 {Species, Sex, Severity, Year, Species*Sex, Sex*Year}	-1465.64	0.52	0.25	14	264.24	0.91
3 {Species, Sex, Severity, Year}	-1464.38	1.78	0.13	8	267.61	0.91
4 {Species, Sex, Severity, Year, Sex*Year}	-1463.76	2.40	0.10	12	265.73	0.91
5 {Species, Sex, Severity, Species*Sex}	-1462.70	3.46	0.06	11	266.50	0.91
6 {Species, Sex, Severity, Year, Species*Sex, Sex*Year, Sex*Severity}	-1462.09	4.07	0.04	16	264.10	0.91
7 {Species, Sex, Severity, Year, Species*Sex, Sex*Year, Species*Severity}	-1461.87	4.29	0.04	16	264.16	0.91
8 {Species, Sex, Severity, Year, Species*Sex, Species*Year, Sex*Year}	-1461.61	4.56	0.03	16	264.22	0.91

[a] Model factors included Species, Sex, Severity (index of spring weather; mean June temperature and total snow depth at end of May and early June), and Year (linear trend with time), and * (asterisk, denotes interaction between variables; otherwise effects are additive).
[b] Akaike's Information Criterion corrected for small sample size.
[c] Difference in AIC_c values between the model with the lowest AIC_c value.
[d] Estimates of the likelihood of the model, given the data; normalized to sum to one (Burnham and Anderson 2002).
[e] Number of estimable parameters.
[f] Sum of squares error of the current model.
[g] Proportion variance explained.

Table 3.2. Top models for variation in protein reserves of breeding female Ross's (n = 341) and snow geese (n = 394) arriving or breeding at the Karrak Lake light goose colony, south of Queen Maud Gulf, Nunavut, Canada, from 1993 to 2008. Only the five top models of forty-six models in the candidate set are shown here, ranked by ascending ΔAIC_c. All other models had ΔAIC_c >16.80.

Number/Model[a]	AIC_c[b]	ΔAIC_c[c]	w_i[d]	K[e]	SSE[f]	R^2[g]
1 {Species, Size, Date, PCTALLOC, CS, Population, Population^2, Species*Population, Species*Population^2}	4505.47	0.00	0.64	14	336299.20	0.86
2 {Species, Size, Date, PCTALLOC, CS, NID, Population, Population^2, Species*Population, Species*Population^2}	4506.76	1.29	0.34	15	335933.94	0.86
3 {Species, Size, PCTALLOC, CS, NID, Population, Population^2, Species*Population, Species*Population^2}	4512.06	7.18	0.02	14	339622.11	0.86
4 {Species, Size, PCTALLOC, CS, Population, Population^2, Species*Population, Species*Population^2}	4518.29	12.83	0.00	13	343236.85	0.86
5 {Species, Size, Date, PCTALLOC, CS, NID, Year, Year^2, Species*Year, Species*Year^2}	4520.17	14.70	0.00	15	342161.23	0.86

[a] Model factors included Species, Population (annual number of breeding individuals at colony in a given year), Population^2 (quadratic effect of population size), Year (linear trend with time), Year^2 (quadratic trend with time), Size (species specific index of body size), PCTALLOC (percentage of total clutch formed at collection period), CS (apparent clutch size of collected females; post ovulatory follicles + developing follicles), NID (annual timing of reproduction for a given year), Severity (index of spring weather; mean June temperature and total snow depth at end of May and early June), Date (collection date of specimen; julian date), and * (asterisk, denotes interaction between variables; otherwise effects are additive).
[b] Akaike's Information Criterion corrected for small sample size.
[c] Difference in AIC_c values between the model with the lowest AIC_c value.
[d] Estimates of the likelihood of the model, given the data; normalized to sum to one (Burnham and Anderson 2002).
[e] Number of estimable parameters.
[f] Sum of squares error of the current model.
[g] Proportion variance explained.

Table 3.3. Top models for variation in abdominal fat of breeding female Ross's (n = 341) and snow geese (n = 394) arriving or breeding at the Karrak Lake light goose colony, south of Queen Maud Gulf, Nunavut, Canada, from 1993 to 2008. Only the top eight models of thirty-nine models from the candidate set are shown, ranked by ascending ΔAIC_c. All other models had $\Delta AIC_c > 4.55$.

Number/Model[a]	AIC_c[b]	ΔAIC_c[c]	w_i[d]	K[e]	SSE[f]	R^2[g]
1 {Species, Size, CS, PCTALLOC, NID, Year, Species*CS, Species*Year}	4263.07	0.00	0.26	13	237259.22	0.51
2 {Species, Size, CS, PCTALLOC, NID, Severity, Year, Species*Year, Species*CS}	4263.94	0.86	0.17	14	236866.24	0.51
3 {Species, Size, CS, PCTALLOC, NID, Population, Species*CS, Species*Population}	4264.37	1.30	0.13	13	237679.67	0.51
4 {Species, Size, CS, PCTALLOC, NID, Year, Species*Year}	4265.54	2.47	0.07	11	239407.56	0.50
5 {Species, Size, CS, PCTALLOC, NID, Severity, Year, Species*Year, Species*CS, Species*Severity}	4265.72	2.65	0.07	16	236094.37	0.51
6 {Species, Size, CS, PCTALLOC, NID, Severity, Population, Species*CS, Species*Population}	4265.76	2.69	0.07	14	237455.71	0.51
7 {Species, Size, CS, PCTALLOC, NID, Severity, Population, Species*CS, Species*Severity, Species*Population}	4265.85	2.78	0.06	16	236137.21	0.51
8 {Species, Date, Size, CS, PCTALLOC, NID, Severity, Population, Species*CS, Species*Severity, Species*Population}	4266.37	3.30	0.05	17	235630.51	0.51

[a] Model factors included species, year (linear trend with time), population (annual number of breeding individuals at colony in a given year), size (species specific index of body size), PCTALLOC (percentage of total clutch formed at collection period), CS (apparent clutch size of collected females; post ovulatory follicles + developing follicles), NID (annual timing of reproduction for a given year), Severity (index of spring weather; mean June temperature and total snow depth at end of May and early June), Date (collection date of specimen; julian date), and * (asterisk, denotes interaction between variables; otherwise effects are additive).
[b] Akaike's Information Criterion corrected for small sample size.
[c] Difference in AIC_c values between the model with the lowest AIC_c value.
[d] Estimates of the likelihood of the model, given the data; normalized to sum to one (Burnham and Anderson 2002).
[e] Number of estimable parameters.
[f] Sum of squares error of the current model.
[g] Proportion variance explained.

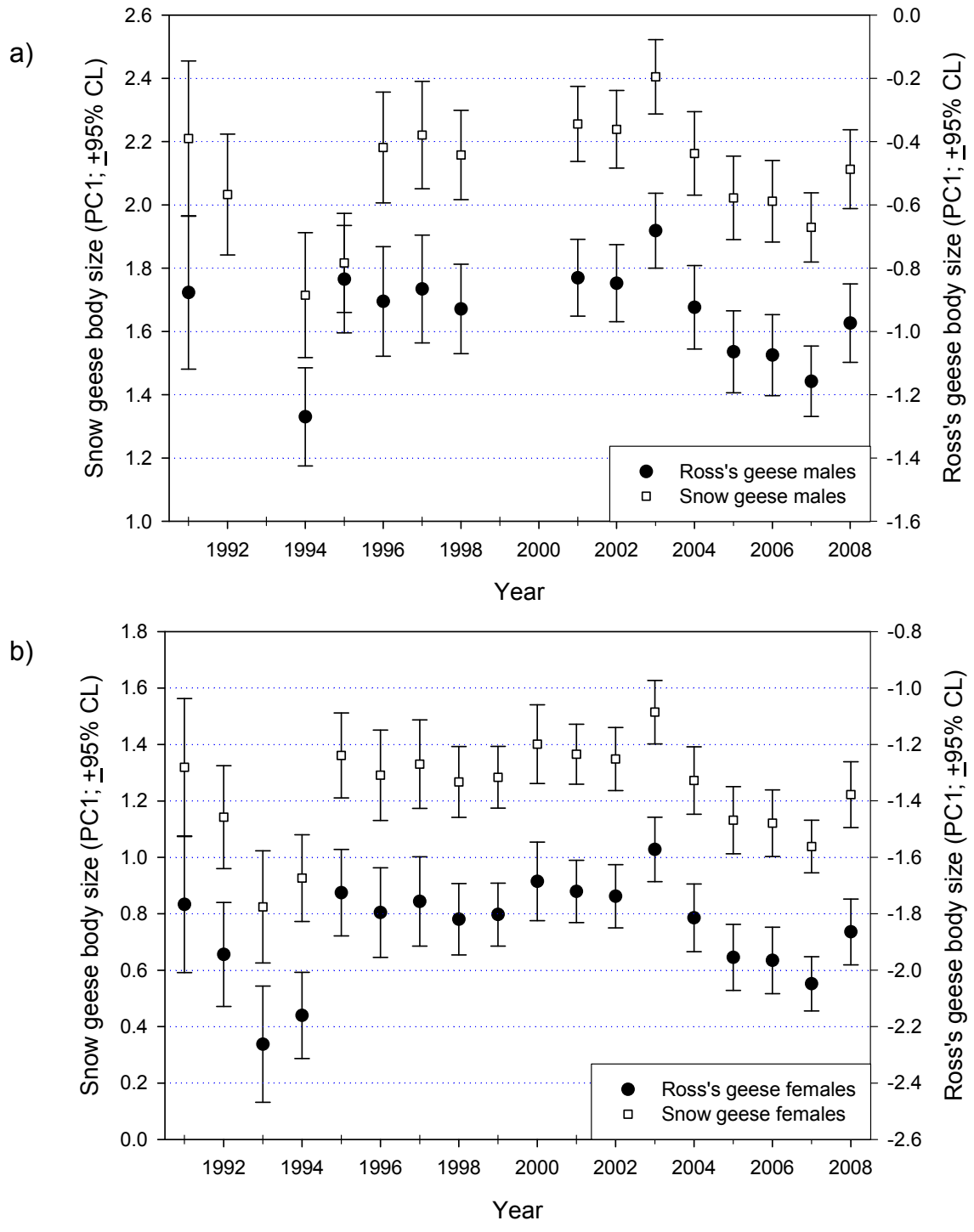


Figure 3.1. Annual mean estimates of body size for male (a) and female (b) Ross's and snow geese arriving or breeding at the Karrak Lake light goose colony, Nunavut, Canada, 1991 to 2008. Snow goose body size estimates are on the left y-axis, while Ross's goose body size estimates are on the right y-axis. Estimates of body size were obtained from a principal components analysis using measurements of tarsus, head length, and wing chord of 1069 geese.

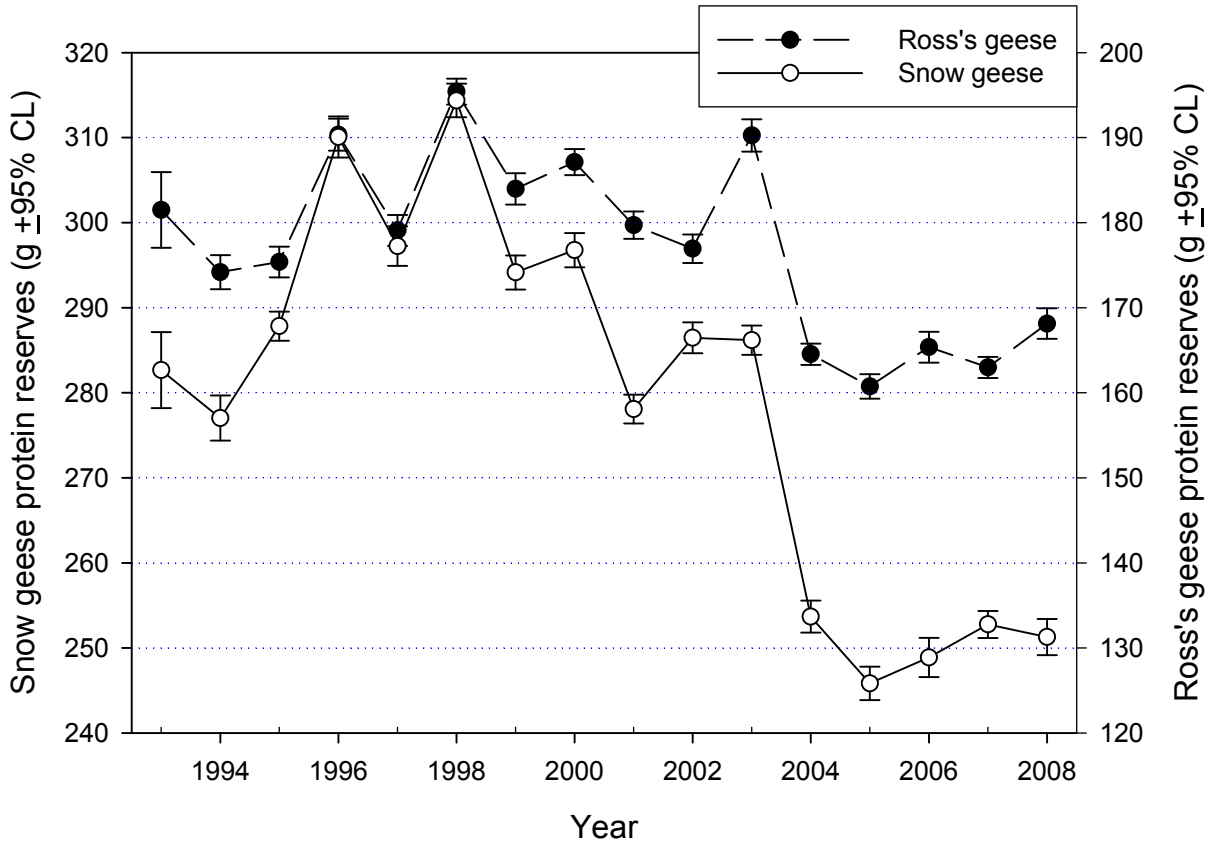


Figure 3.2. Annual mean estimates of protein reserves for breeding female Ross's (n = 341) and snow (n = 394) geese arriving or breeding at the Karrak Lake light goose colony, south of Queen Maud Gulf, Nunavut, Canada, from 1993 to 2008. Snow goose protein reserve estimates are on the left y-axis, while Ross's goose protein reserve estimates are on the right y-axis. I used the mass (g) of one breast muscle and one bone-free leg muscle as an index of body protein.

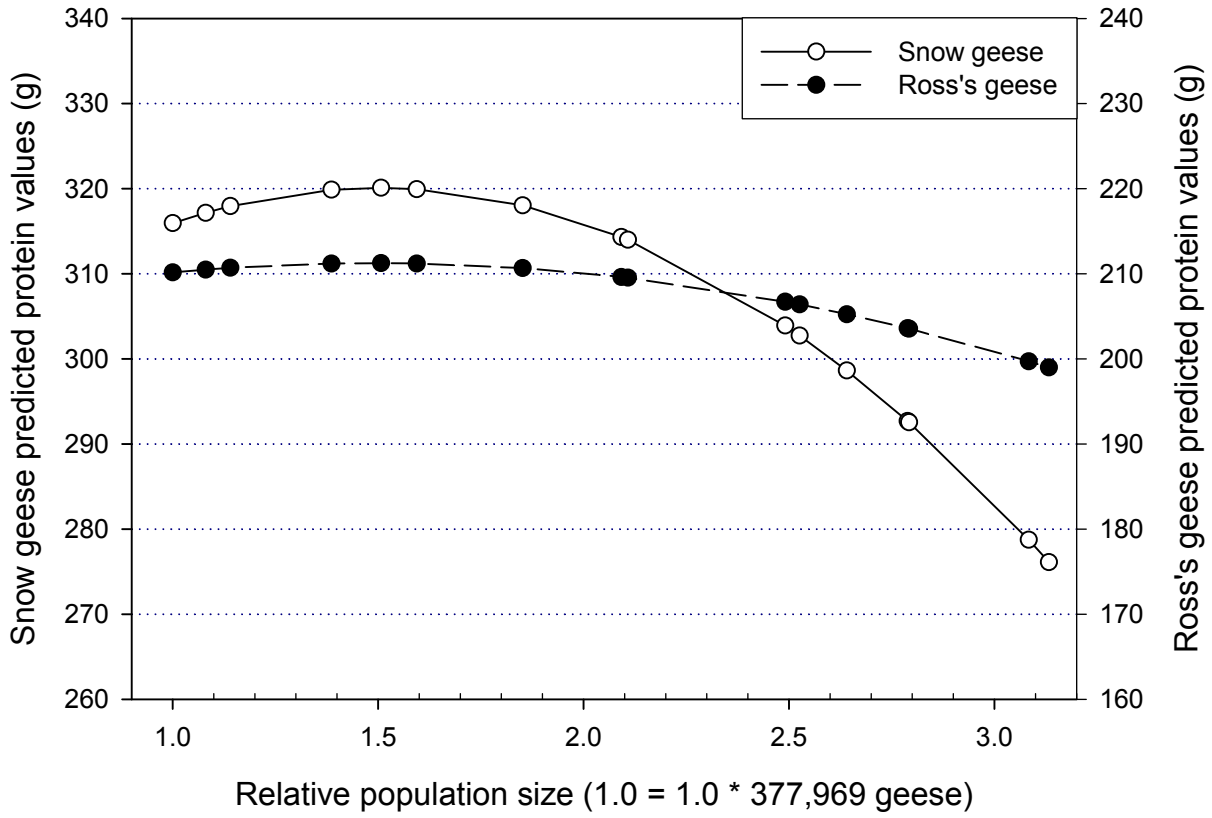


Figure 3.3. Predicted relationship of population size on protein reserves for breeding female Ross's and snow geese arriving or breeding at the Karrak Lake light goose colony, south of Queen Maud Gulf, Nunavut, Canada. Snow goose predicted protein reserve estimates are on the left y-axis, while Ross's goose predicted protein reserve estimates are on the right y-axis. Slope estimates are based on weighted model averaged estimates of $\overline{\hat{\beta}}_{pop(snow)} = 49.94$; $\overline{\hat{\beta}}_{pop^2(snow)} =$ -16.51 and $\overline{\hat{\beta}}_{pop(ross)} = 13.56$; $\overline{\hat{\beta}}_{pop^2(ross)} =$ -4.55 for snow and Ross's geese, respectively. Relative population size is an annual population estimate of the breeding colony divided by the lowest estimate of 377,956 breeding geese in 1994.

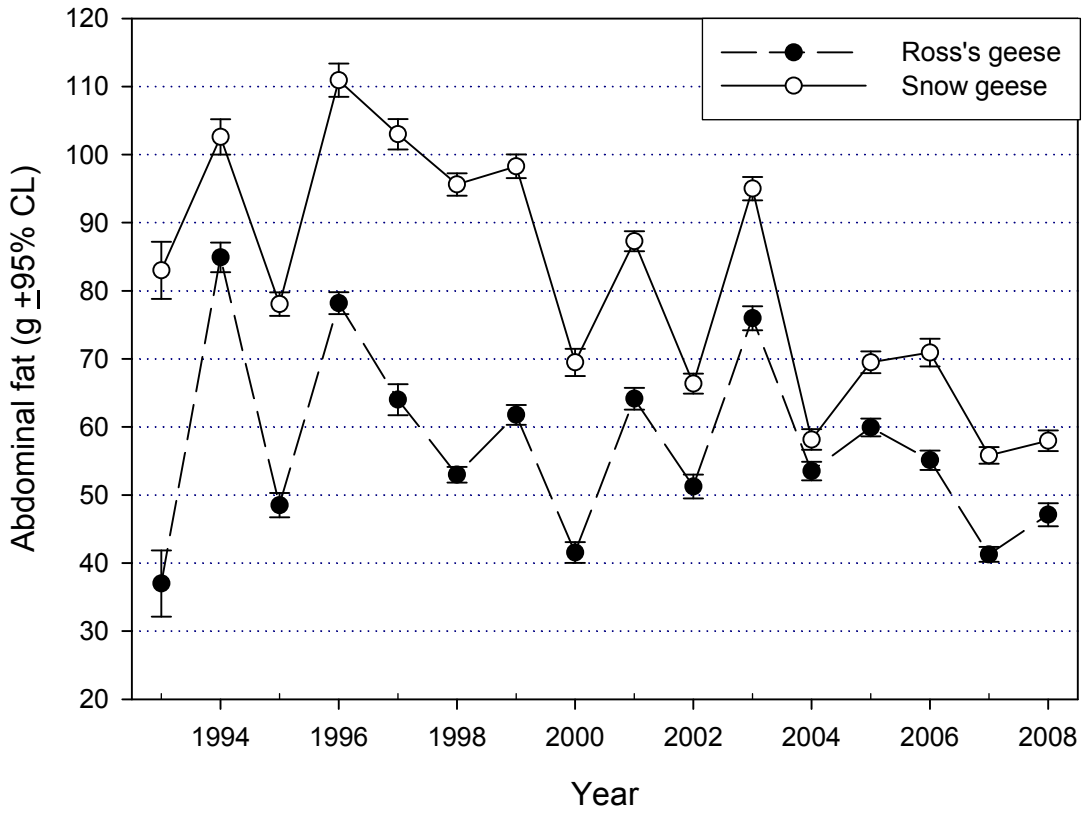


Figure 3.4. Annual mean estimates of abdominal fat reserves for breeding female Ross's (*n* = 341) and snow (*n* = 394) geese arriving or breeding at the Karrak Lake light goose colony, south of Queen Maud Gulf, Nunavut, Canada, from 1993 to 2008. The mass (g) of abdominal fat was used as an index of total fat reserve.

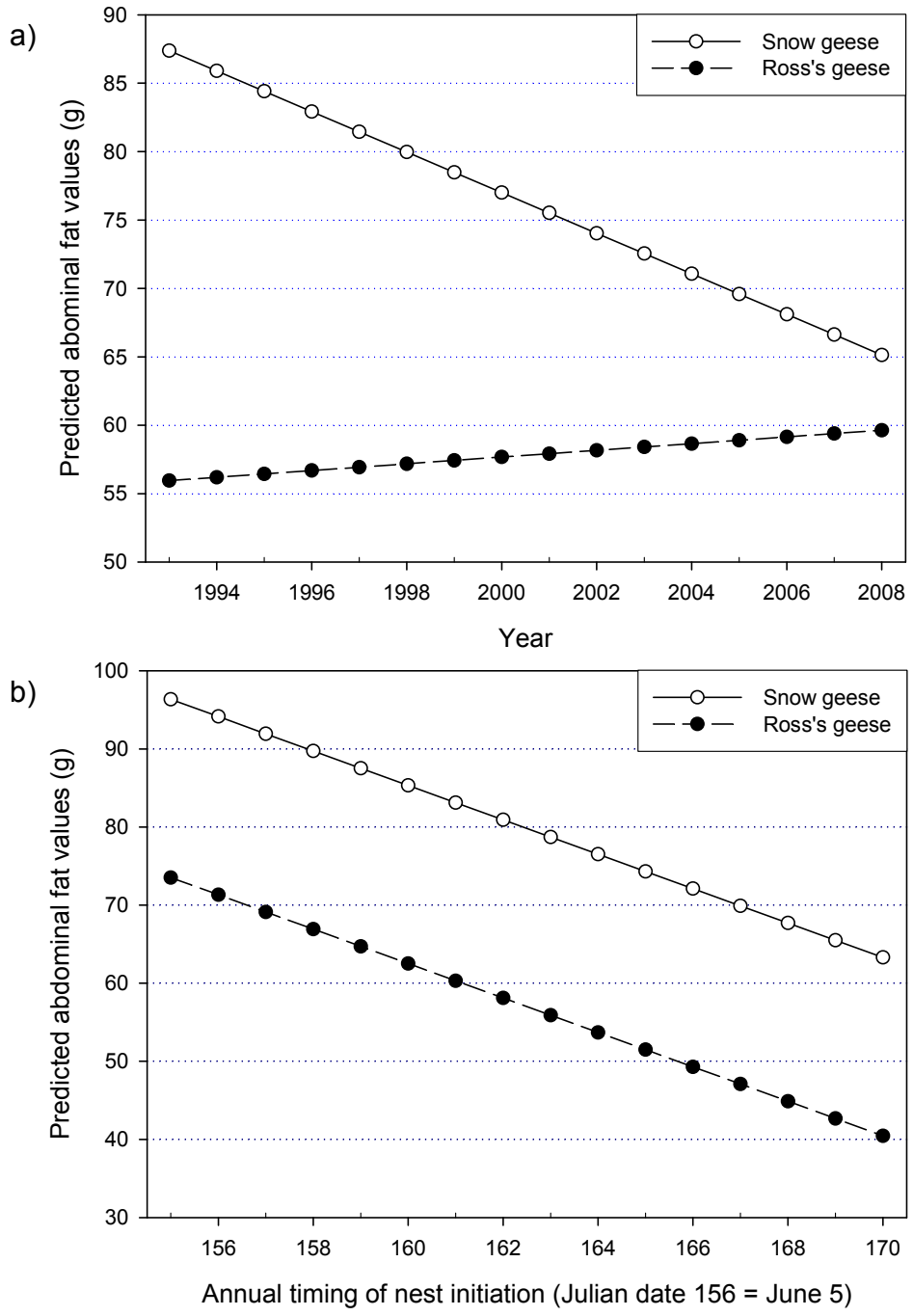


Figure 3.5. Predicted relationships of a) year (linear time trend) and b) annual timing of breeding on abdominal fat reserves of breeding female Ross's and snow geese arriving or breeding at the Karrak Lake light goose colony, Nunavut, Canada. Slope estimates for year are based on weighted model averaged estimates of $\overline{\hat{\beta}}_{year(snow)} = -1.48$ and $\overline{\hat{\beta}}_{year(ross)} = 0.25$ for snow and Ross's geese, respectively. The slope estimate for an additive effect of timing of breeding was based on weighted model averaged estimate of $\overline{\hat{\beta}}_{NID} = -2.20$.

4. ISOTOPIC ASSESSMENT OF NUTRITIONAL STRATEGIES FOR EGG PRODUCTION BY DIFFERENT-SIZED ARCTIC GEESE

4.1 INTRODUCTION

Understanding nutrient dynamics during reproduction can provide insight regarding life history variation since the manner in which animals use their food supply can have significant consequences for fitness (Stearns 1992). For some migratory species, access to food can be unpredictable during breeding, leading to a dependence of reproductive success on size of nutrient stores and timing of reproduction (Ankney and Alisauskas 1992a). Accordingly, breeding strategies have evolved ranging along a continuum from a dependence on endogenous nutrients by capital breeders to complete reliance on exogenous foods processed directly into egg components by income breeders (Drent and Daan 1980, Jönsson 1997, Bonnet et al. 1998). Capital breeders transport nutrients for reproduction which represents a considerable adaptation as storage allows feeding and reproduction to be decoupled spatially and temporally (Jönsson 1997). Thus, capital breeding is favorable within unpredictable environments or those with predictably low food supply because individuals can enhance likelihood of reproductive success by avoiding delays in breeding (Ankney and MacInnes 1978, Raveling 1979a, b, Jönsson 1997). However, costs can arise from constraints of storage, transport, and maintenance of stores (Jönsson 1997). By contrast, income breeders supply nutrients for reproduction directly from breeding grounds. This can be advantageous in predictable habitats, although sometimes resources may be insufficient to meet costs of metabolism and reproduction (Jönsson 1997, Bonnet et al. 1998).

Arctic-breeding geese have mixed breeding strategies and their position within the capital/income continuum has remained a topic of debate i.e., the traditional view of transporting reserves from afar for egg production (Ryder 1970, Ankney and MacInnes 1978) being confronted with the view that exogenous nutrients contribute more to egg production than do reserves (Budeau et al. 1991, Gauthier et al. 2003). Recently, a refined definition of capital breeding acknowledged the distance between storage and use of capital. Distant capital is obtained from afar, perhaps in an ecosystem different from the one in which breeding occurs, while local capital is obtained near the breeding site and in the same kind of ecosystem but

perhaps 50 to 100 km from the breeding site (Klaassen et al. 2006, Drent et al. 2007). Additionally, local capital might involve the storage of reserves from the same area, but preceding the breeding attempt, such as can be done by ruddy ducks (*Oxyura jamaicensis*) or lesser scaup (*Aythya affinis*) (Alisauskas and Ankney 1994, Afton and Ankney 1991); but this may change as ecosystem supply of preferred foods change (Anteau and Afton 2009). In any case, the position of a species within the capital/income continuum can be important to reproductive success because factors that influence breeding performance can be different between species that rely on stored food or breeding ground forage (Choinière and Gauthier 1995, Alisauskas 2002, Fèret et al. 2003). Breeding strategies among waterfowl, ultimately, represent a tradeoff between nutrients available for clutch formation and incubation (Alisauskas and Ankney 1992a). For this reason, dynamic strategies should be evident in arctic-breeding species given that access to forage may be unpredictable.

There is a general interspecific relationship between size and breeding strategies among animals (Raveling 1978, 1979, Afton 1980, Meijer and Drent 1999). Smaller species are generally thought to be greater income breeders because they carry fewer endogenous reserves and have a proportionately higher metabolism than larger species (Calder 1974, Afton 1980). Thus, Ross's geese (*Chen rossii*) are predicted to rely more on income breeding than lesser snow geese (*Chen caerulescens caerulescens*, hereafter snow geese) which are about 50% heavier. In support of this prediction, Gloutney et al. (2001) found that Ross's geese spend more time foraging than snow geese during nesting. However, migratory schedules can also influence breeding strategies (Klaassen et al. 2006). Larger species require longer breeding seasons, so they often arrive earlier onto breeding grounds and are predicted to be greater income breeders than small species (Klaassen et al. 2006). Despite being the largest of the three congeners, Gauthier et al (2003) concluded that greater snow geese displayed a predominantly income breeding strategy. Thus, smaller species may rely more on capital breeding than larger species to offset time constraints of later arrival on successful production of young in a highly seasonal environment (Raveling 1978, Klaassen et al. 2006).

I examined variation in nutritional strategies of breeding Ross's and snow geese by estimating proportional contributions of endogenous and exogenous nutrients to clutch formation, inferred from stable isotope analysis of eggs, tissues and foods of female geese (Gauthier et al. 2003). I used Program SISUS (Stable Isotope Sampling using Sourcing;

http://statacumen.com/sisus/) to estimate the proportion of exogenous and endogenous nutrients used in the formation of first and last eggs of a clutch. To reveal the extent of *local* capital breeding in these arctic geese, I compared breeding strategies and isotopic signatures of tissues and eggs from birds that recently arrived onto the colony with those that had commenced incubation. Finally, I examined interspecific differences in mass change of goose tissues during breeding to estimate absolute supply of endogenous nutrients.

Ross's and lesser snow geese are closely related (99.7% similarity of DNA) (Avise et al. 1992, Hebert et al. 2004) and breed sympatrically in large shared colonies so that phylogeny and breeding environment, that could additionally influence breeding strategy, are controlled for. Both species initiate rapid follicle growth (RFG) during late spring migration and most begin egg-laying within 3 days after arrival. Consequently, the short time lag between arrival and initiation of laying (Ryder 1972, Raveling 1978, Gloutney et al. 2001) constrains the opportunity to exploit local foods at nesting areas. Snow geese arrive onto the Karrak Lake, Nunavut, Canada breeding colony from their spring migration between 25 May and 15 June while Ross's geese have a different chronology, arriving $\geq$3 days later (Bon 1997, Alisauskas 2002). Consequently, Ross's geese initiate nesting 2 to 4 days later than snow geese, which are already laying (Slattery and Alisauskas 1995). I tested two mutually-exclusive hypotheses to explain differences in breeding strategies used in clutch formation between species. The body size hypothesis predicts greater capital breeding in snow geese because they are structurally larger whereas the migratory schedule hypothesis predicts greater capital breeding in Ross's geese since they arrive later onto the breeding areas. If these species are predominantly capital breeders and there are differences in isotopic values of their respective endogenous depots then differences should be reflected in isotopic values of egg constituents. However, since the diet of each species is much the same, if they predominantly use local foods for eggs, then interspecific difference in egg components should be absent.

4.2 METHODS

4.2.1 Sample collection

Mean nest initiation dates in 2004 were similar to the long-term mean (1991-2005, Ross's geese = 11 June and snow geese = 9 June) for Ross's (12 June) and snow (8 June) geese, respectively

(Alisauskas unpubl. data). However, in 2005 nest initiation was 3-4 d earlier for both Ross's (8 June) and snow (5 June) geese.

I collected arriving adult female Ross's and snow geese with a shotgun in 2004 (8-13 June, n = 25 snow geese and n = 25 Ross's geese) and 2005 (4-14 June, n = 27 snow geese and n = 29 Ross's geese). I assumed my sample of arrivals had just reached the breeding colony because I only targeted birds seen flying from the southwest (general direction from birds fly to reach colony); once birds arrive onto the colony they are generally confined to their nesting territory (Ryder and Alisauskas 1995). Next, I also collected adult female Ross's and snow geese from their nest early in incubation with a rifle in 2004 (17-18 June, n = 23 snow geese and n = 22 Ross's geese) and 2005 (13-18 June, n = 20 snow geese and n = 21 Ross's geese). Early incubation birds were collected from nests that had been incubated < 6 days. A sample of birds at mid-incubation (day 7 to 10) were collected on their nest in 2005 (21 June, n = 15 snow geese and n = 15 Ross's geese). Finally, I collected birds during the hatching period (day 17 to 23 of incubation) from their nests in 2004 (3-5 July, n = 20 snow geese and n = 22 Ross's geese) and 2005 (2 July, n = 20 snow geese and n = 20 Ross's geese).

I collected the first and last eggs laid in each nest sampled (from early incubation birds only) (Gauthier et al. 2003) since I expected maximum differences in isotopic signatures between these (Schmutz et al. 2006). Laying order of eggs was determined by egg color (staining; first egg dirtiest and last egg cleanest) (Gauthier et al. 2003), although if an oviducal egg (n = 2) was present in early incubation birds, it was considered the last egg. I obtained nest initiation dates by backdating incubation stage (Weller 1956) and clutch size based on mean laying intervals for these species (Ryder and Alisauskas 1995, Mowbray et al. 2000). Birds were dissected at camp and samples of liver, breast, and abdominal fat were stored in 70% ethanol until preparation for stable isotope analysis (Gloutney and Hobson 1998). I removed ovaries to count developing follicles and postovulatory follicles in arrival birds to obtain real clutch size values for each bird. The largest developing follicle (~27.0 g w/w) or oviducal egg, if present, was removed from arrival birds for isotopic analysis. In early incubation birds, I counted postovulatory follicles, presence of oviducal eggs, and order of eggs in the nest so that the exact laying sequence of eggs could be ascertained (see Gauthier et al. 2003). Following Gauthier et al. (2003), if there were more postovulatory follicles than eggs in the nest I assumed that missing eggs were the first eggs laid as these are most vulnerable to predation. However, Mowbray et al. (2000) also suggest first

eggs are frequently abandoned as 'dump' eggs on the colony or during late spring migration (Bon 1997). There were 21 cases out of 116 that had fewer eggs in the nest (and oviduct) than there were postovulatory follicles. Occasionally, there were instances (6 cases) where there were more eggs (including any oviducal eggs) than postovulatory follicles; these nests were considered to have been parasitized. The mean position of early and late laid eggs used in analyses was 1.2 and 3.5, respectively; hereafter I refer to early eggs as first laid eggs and late laid eggs as last laid eggs. Eggs and developing follicles were boiled, and eggs were manually separated into shell, yolk and albumen, placed in plastic bags, and frozen for shipment to the laboratory. After dissection, I recorded mass of breast muscle, leg muscle, liver and gizzard, whose cumulative mass was used as an index of body protein, and abdominal fat depot as a measure of fat reserve. A sample of breast muscle and abdominal fat from each bird was saved for isotope analysis. To obtain a breeding ground (exogenous) isotopic signal, I collected local food plants consumed by geese (Gloutney et al. 2001). Vegetation samples were collected in the Karrak Lake colony during egg laying. Vegetation was subsequently dried to a constant mass and placed in paper envelopes for shipment to the laboratory.

4.2.2 Laboratory analyses

Samples for isotope analysis of breast muscle, liver, abdominal fat, egg yolk (including developing follicles), and albumen were dried at 60°C until constant mass was reached (Gloutney and Hobson 1998). Breast muscle and yolk samples were then rinsed repeatedly in a 2:1 chloroform: methanol solution to remove lipids and placed under a fume hood to air dry. Dried liver (whole), breast, albumen, and lipid-free yolk (which I refer to as 'yolk protein', hereafter) samples were then ground to a powder with a mortar and pestal. One developing follicle or oviducal egg and 2 eggs were each analyzed from arrival and early incubation birds, respectively. Yolk lipid and abdominal fat were used as measures of lipids, while dry albumen, yolk protein, dry breast muscle, and whole dry liver were used as measures of protein. Food plants available to geese at time of nesting included bearberry (*Arctostaphylos* spp.), chickweed (*Stellaria* spp.), cranberry (*Vaccinium vitis-idaea*), crowberry (*Empetrum nigrum*), Labrador Tea (*Ledum decumbens*), moss (Bryophytes), and sedge (*Carex* spp.) (Gloutney et al. 2001). Foods were ground into powder samples with a mortar and pestal. Samples of ~1 mg for goose tissues/eggs and 2 to 5 mg for foods were weighed, place in tin cups and combusted in a Europa

20:20 continuous flow ratio mass spectrometer (CFIRMS) at the Department of Soil Sciences at the University of Saskatchewan to obtain stable-carbon and stable-nitrogen isotopes ratio values. I used laboratory standards of egg albumen and whale baleen for every 5 tissue and/or egg samples analyzed; pea-green standard was used for food sample N since vegetation has relatively low percent N. Ratios of stable isotopes were expressed in δ-notation as parts per thousand (‰) deviations from Pee Dee Belemnite ($\delta^{13}C$) and atmospheric air ($\delta^{15}N$) standards according to $\delta X = [(R_{sample}-R_{standard})/R_{standard}] \times 1000$, where X is ^{13}C or ^{15}N and R is $^{13}C/^{12}C$ or $^{15}N/^{14}N$. Laboratory measurement error was ±0.1‰ for $\delta^{13}C$ and ±0.3‰ for $\delta^{15}N$.

4.2.3 Discrimination factors and isotopic calculations

I used the herbivore model from Hobson (1995) for local food plants to egg discrimination values (+3.4‰ to yolk protein and albumen $\delta^{15}N$ values, 0‰ to yolk protein and +1.5‰ to albumen $\delta^{13}C$ values, and -2.6‰ to yolk lipid $\delta^{13}C$ values). I then corrected for discrimination between somatic reserves and egg constituents. I applied a $\delta^{13}C$ discrimination factor of -3.2‰ for abdominal fat to yolk lipid (Hobson 1995, see Appendix). For yolk protein and albumen, I corrected discrimination by adding +0.87‰ to the $\delta^{15}N$ values and applied a value of -0.1‰ to the $\delta^{13}C$ values of breast muscle (Hobson 1995, Fantle et al. 1999, Vanderklift and Ponsard 2003, see Appendix). I used only eggs collected early in incubation to avoid possible discrimination that may occur as incubation progresses (Sharp et al. 2009).

I used Program SISUS (Stable Isotope Sourcing Using Sampling) to estimate breeding strategies. SISUS is a Bayesian statistical model, which incorporates variation in isotope signatures in sources and mixtures to produce results. SISUS can account for source discrimination, concentration of nitrogen and carbon, assimilation efficiency, linear constraints, and prior information (see http://StatAcumen.com/sisus, Erhardt et al. unpubl. manuscript). To calculate the contribution of endogenous (capital) and exogenous (income) sources to clutch formation I used the mean $\delta^{15}N$ and $\delta^{13}C$ signature and standard deviation for egg constituents from 1) arriving females and their largest developing follicles or oviducal eggs, and early incubation females and their 2) first-laid and 3) last-laid egg within a clutch (Tables 4.1 and 4.2). Egg components (albumen, yolk protein and yolk-lipid) for each species and group per year were analyzed separately in SISUS resulting in 36 models. I considered the contribution of five sources to yolk protein and albumen, explained below. I used the mean and standard deviation of lipid free

breast $\delta^{15}N$ and $\delta^{13}C$ signature as the endogenous source of protein (Tables 4.1 and 4.2). For exogenous source signals, I used mean $\delta^{15}N$ and $\delta^{13}C$ signatures and standard deviations from four foods that included sedge, chickweed, moss, and shrubs (bearberry, cranberry, crowberry, and Labrador tea) (Table 4.3). Shrubs were grouped to reduce the total number of sources since they were not an important diet item (Gloutney et al. 2001; Phillips and Gregg 2003). Further, shrubs had similar $\delta^{13}C$ signatures ($P = 0.74$), although there were slight difference in $\delta^{15}N$ signatures ($P = 0.04$). Lipid has little or no N, so $\delta^{15}N$ of lipids was not considered. The mean $\delta^{13}C$ signature and standard deviation of abdominal fat was used as the source of endogenous reserves for yolk lipid, while the mean $\delta^{13}C$ signatures of each of the four food groups were used as exogenous signals.

In structuring SISUS for each mixture (i.e., albumen, yolk protein and yolk-lipid) I used default settings specifying how samples were collected (M = the total number of samples to retain, skip = Markov chain Monte Carlo sampling procedure in which every specified value is skipped, burnin = number of samples before retention for analysis, and seed = seed to initialize the random number generator) as these were judged *a priori* to be appropriate (see http://StatAcumen.com/sisus). Then, I included the simplex constraint to restrict the proportional contributions of my sources to be equal to 1. Next, I applied the appropriate discrimination factors to my sources. I did not include concentration dependence in my models since in preliminary analyses incorporating concentration dependence produced unrealistic results (i.e., $\geq$ 100% income or capital breeder or negative results). Recent comparisons of the three main types of isotopic models (mass balance mixing models, concentration-dependent linear mixing model, and IsoSource [comparable to SISUS when structured similarly]) suggest model choice is particularly important; concentration-dependent linear mixing models produced the most biased results (Caut et al. 2008). Next, I did not include linear constraints on sources as I assumed equal importance of each food item because arctic climate is unpredictable and relative importance likely varies annually (Gauthier et al. 2003). Additionally, I chose not to incorporate prior information (expert opinion) as this was the first time this type of analysis was to be done on these two goose species. Hence, I allowed all combinations that sum to 1 (simplex constraint) to be equally likely (see http://StatAcumen.com/sisus). Finally, I entered in the standard deviations for sources and mixtures, although they were only used in graph plots. In some cases yolk lipid estimates in SISUS did not converge as the mixture was outside the source bounds.

Consequently, I used simple linear regression to generate expected breeding strategy values based on the relationship between proportion capital breeding and discrimination factors (see Appendix). I present results as percent capital breeders (range 0 to 100%); estimates of income breeding are equal to 100% minus percent capital breeding.

4.2.4 Statistical analyses

I followed hierarchical procedures in MANCOVA and ANCOVA such that final models only contain significant variables (Alisauskas and Ankney 1994); least-squares means were obtained from these models. All general linear models (Proc GLM) used Type III sums of squares. Statistical significance was evaluated against an $\alpha = 0.05$; 95% confidence limits ($\pm$95% CL) are presented throughout unless stated otherwise. Statistical analyses were done using SAS version 9.1 (SAS Institute 2008).

I performed species-specific analysis of covariance (ANCOVA) to examine if isotopic signatures of breast muscle and abdominal fat (i.e., endogenous reserves) changed as arrival date and incubation stage progressed for arrival and early-incubation birds since this could be a confounding factor in my analyses. There were no differences in tissues (breast muscle or abdominal fat; all $P \geq 0.24$), so arrival date and incubation stage were ignored in all further analyses. Thus, for all future analyses early incubation birds are equivalent to post-laying birds. Mean incubation stage at collection for early-incubation birds was 1.82 d and 3.62 d for Ross's geese and 3.82 d and 2.20 d for snow geese in 2004 and 2005, respectively. I used general linear models to examine differences in isotopic signatures in 1) local food plants and 2) among local food plants and endogenous reserves.

I used multivariate analysis of covariance (MANCOVA) with post-hoc Tukey Studentized tests to assess overall species differences in isotope values of 1) tissues (breast muscle, abdominal fat, and liver) and 2) egg components (albumen, yolk protein, and yolk lipid) of birds collected at early incubation with year as a covariate and a species*year interaction. *F*-values reported from MANCOVA were determined using Wilks' criterion. I then used species-specific analysis of variance (ANOVA) to examine annual differences in 1) tissues and 2) egg components for each species separately. I used MANCOVA with post-hoc Tukey Studentized tests to examine overall status (arriving or incubating) changes in isotope values of 1) tissues and 2) egg components with species and year as covariates and two-way interactions. I then performed

species-specific ANCOVA to examine differences in 1) tissues and 2) egg components between arrival and early-incubation birds with year as covariate and a status*year interaction. To examine laying sequence differences, I used a paired t-test (Proc t-test) to examine isotopic differences between first and last laid eggs within a clutch for each species and year separately. Finally, to examine the use of reserves for breeding, I performed two analyses. First, I performed species specific ANCOVA to examine relationships between mass of body, breast muscle, leg muscle, abdominal fat, liver, gizzard, total protein (i.e., sum of leg, breast, liver, and gizzard mass) and status (i.e., arrival, early incubation, mid-incubation, and late-incubation) while controlling for year. Then, I performed species specific ANCOVA to examine relationships between isotopic signal of breast muscle, abdominal fat, and liver and status (i.e., arrival, early incubation, and mid-incubation) while controlling for year. I compared least square means among status types with t-tests (PDIFF option).

4.3 RESULTS

4.3.1 Isotopic signatures of foods, goose tissues and eggs

Local arctic food plants differed in isotopic signatures ($\delta^{13}C$ signatures $F_{3,34} = 8.21$, $P = 0.0004$; $\delta^{15}N$ signatures $F_{3,34} = 16.60$, $P < 0.0001$) (Table 4.3). Food plant signatures ($\delta^{13}C$ and $\delta^{15}N$) were considerably different from those of endogenous reserves (breast and abdominal fat) (all $P \leq 0.0001$; Tables 3.2 and 3.3). Both $\delta^{13}C$ and $\delta^{15}N$ signatures of food plants were significantly more depleted than endogenous reserves (Tables 3.2 and 3.3).

There were differences in tissue isotopic signatures between Ross's and snow geese. Specifically, breast $\delta^{13}C$ values of Ross's geese were more depleted (Ross's = -23.91, snow = -22.44; species effect, Wilks' $\lambda = 0.56$, $F_{1,84} = 64.80$, $P < 0.0001$). In breast $\delta^{15}N$ and liver $\delta^{13}C$ values there were differences but they changed annually. Breast $\delta^{15}N$ (species*year interaction, Wilks' $\lambda = 0.91$, $F_{1,82} = 7.38$, $P = 0.008$) values of Ross's geese were significantly more depleted than snow geese in 2004 (Ross's = 6.35, snow = 6.97; $P = 0.0008$), though there were no differences in 2005 (Ross's = 6.85, snow = 6.86; $P = 0.99$). Liver $\delta^{13}C$ (species*year interaction, Wilks' $\lambda = 0.92$, $F_{1,82} = 6.91$, $P = 0.01$) values of Ross's geese were significantly more depleted than snow geese in both years though differences were greater in 2004 (2004 Ross's = -25.28, snow = -24.06, $P < 0.0001$; 2005 Ross's = -24.93, snow = -24.41, $P = 0.03$). There were no differences between Ross's and snow in liver $\delta^{15}N$ (Ross's = 7.82, snow = 7.90;

species effect, Wilks' $\lambda = 0.99$, $F_{1,83} = 0.36$, $P = 0.55$) or abdominal fat $\delta^{13}C$ values (Ross's = -25.35, snow = -24.93; species effect, Wilks' $\lambda = 0.97$, $F_{1,84} = 2.18$, $P = 0.14$). Species-specific analyses indicated $\delta^{13}C$ values of goose tissues displayed little variation between years (Table 4.2). There were no differences in breast, abdominal fat, or liver among years in Ross's geese (all $P \geq 0.11$). Snow geese followed the same pattern with no variation among years in breast or abdominal fat (all $P \geq 0.18$), although there was a slight difference in liver ($F_{1,42} = 4.89$, $P = 0.03$) between years. There were few differences in $\delta^{15}N$ signatures of goose tissues between years (Table 4.2). Geese exhibited no annual differences in breast or liver (all $P \geq 0.40$), though Ross's geese had significantly different breast values among years ($F_{1,42} = 13.01$, $P = 0.0008$).

Similarly, there were differences in isotopic signatures of egg components between Ross's and snow geese. Specifically, there were differences in $\delta^{13}C$ values of egg constituents. Albumen of Ross's geese was more depleted than that of snow geese (Ross's = -24.88, snow = -24.26; species effect, Wilks' $\lambda = 0.61$, $F_{1,83} = 53.47$, $P < 0.0001$). Yolk protein of Ross's geese, while controlling for a significant year effect (year effect, Wilks' $\lambda = 0.94$, $F_{1,82} = 5.08$, $P = 0.03$), was more depleted than that of snow geese (Ross's = -24.70, snow = -24.25; species effect, Wilks' $\lambda = 0.75$, $F_{1,82} = 27.78$, $P < 0.0001$). However, differences in yolk lipid values between species changed annually (species*year interaction, Wilks' $\lambda = 0.82$, $F_{1,81} = 17.10$, $P < 0.0001$). In 2004, Ross's geese had more depleted values (Ross's = -28.99, snow = -28.22, $P = 0.0016$), while in 2005 there were no differences (Ross's = -28.35, snow = -28.79, $P = 0.16$). There were no differences between species in albumen $\delta^{15}N$ (Ross's = 6.58, snow = 6.78; species effect, Wilks' $\lambda = 0.99$, $F_{1,83} = 1.11$, $P = 0.30$) or yolk protein $\delta^{15}N$ (Ross's = 7.04, snow = 7.11; species effect, Wilks' $\lambda = 0.99$, $F_{1,83} = 0.10$, $P = 0.75$) values of egg constituents. Further univariate comparisons revealed that $\delta^{13}C$ values of egg constituents showed slight annual variation (Table 4.2). In Ross's geese, there were no annual differences in albumen or yolk protein (all $P \geq 0.28$), still there was annual variation in yolk lipid ($F_{1,42} = 8.91$, $P = 0.005$). Snow geese displayed no difference in albumen ($F_{1,42} = 0.11$, $P = 0.74$), although there was annual variation in yolk protein ($F_{1,42} = 4.38$, $P = 0.04$) and yolk lipid ($F_{1,42} = 8.25$, $P = 0.006$). The $\delta^{15}N$ values of egg constituents were similar between years (Table 4.2). In both species, there were no differences in albumen or yolk protein (all $P \geq 0.16$). Overall, differences in isotopic signatures of egg components between species reflected the differences in reserve constituents between species (i.e., tissues of Ross's geese more depleted thus egg constituents

more depleted). Because each species likely has a similar local diet, if geese used local food resources for egg production then interspecific differences in egg components would be absent.

4.3.2 Allocation of nutrient reserves to eggs

Endogenous reserves contributed the largest portion to yolk protein (86% and 75%) and yolk lipid (85% and 95%) in both years for Ross's geese (Table 4.4). However, synthesis of albumen depended on a mixed strategy; endogenous contributions were 54% and 52% in both years (Table 4.4). Moss (25% and 25%) and shrubs (10% and 11%) were important (≥ 10%) exogenous contributors to albumen production in 2004 and 2005, respectively (Table 4.4). Likewise, snow geese used mostly endogenous reserves for production of yolk protein (69% and 62%) and yolk lipid (86% and 73%) in 2004 and 2005, respectively (Table 4.5). Conversely, endogenous reserve contribution to albumen synthesis was similar to exogenous contribution (50% and 48%) in both years (Table 4.5), as found for Ross's geese. Moss (18% and 23%), *Carex* spp. (14% and 10%), and shrubs (10% and 13%) were important exogenous contributors to albumen synthesis by snow geese in 2004 and 2005, respectively (Table 4.5). Regardless of year effects, Ross's geese partitioned large amounts of endogenous reserves into yolk protein and yolk lipid. Overall, Ross's geese partitioned 17% more of their endogenous reserves to yolk protein than did snow geese in 2004, while in 2005 they partitioned more endogenous reserves to yolk protein (13%) and yolk lipid (22%).

4.3.3 Evidence for capital breeding: Isotope ratios of arrival and early incubation individuals

Multivariate analyses showed that isotopic signatures of tissues changed between arrival (= A) and incubation (= I). After controlling for a species effect (Wilks' $\lambda = 0.92$, $F_{1,189} = 17.30$, $P < 0.0001$), abdominal fat $\delta^{13}C$ enriched (A = -25.77, I = -25.15; status effect, Wilks' $\lambda = 0.95$, $F_{1,189} = 10.76$, $P = 0.0012$). Local foods were depleted in isotope values compared to goose tissues so enrichment of tissues from arrival to incubation indicated increased reliance on endogenous reserves after reaching the colony. Concurrently, liver $\delta^{15}N$ values also enriched (A = 7.86, I = 6.65; status effect, Wilks' $\lambda = 0.56$, $F_{1,190} = 148.65$, $P < 0.0001$). After accounting for significant year effects (year effect, Wilks' $\lambda = 0.98$, $F_{1,187} = 4.31$, $P = 0.04$), liver $\delta^{13}C$ enriched after arrival as well, but enrichment was greater in snow geese than in Ross's geese

(status*species interaction, Wilks' $\lambda = 0.90$, $F_{5,183} = 3.98$, P = 0.002): enrichment was 0.87‰ in snow geese (A = -25.09, I -24.22; P < 0.0001) but only 0.39‰ in Ross's geese (A = -25.51, I = -25.12; P = 0.03). There were no differences between arrival and incubating birds in breast $\delta^{13}C$ (A = -23.12, I = -23.18; status effect, Wilks' $\lambda = 0.99$, $F_{1,187} = 0.15$, P = 0.70) or breast $\delta^{15}N$ (A = 6.61, I = 6.76; status effect, Wilks' $\lambda = 0.98$, $F_{1,188} = 3.91$, P = 0.05) values. Univariate analyses revealed differences within species. In Ross's geese, there was no effect of status on breast $\delta^{15}N$ or $\delta^{13}C$ values (all $P \geq 0.45$) (Figs. 4.1 and 4.3). However, there was significant enrichment between arrival and early incubation in abdominal fat $\delta^{13}C$ (A = -26.32, I = -25.36; $F_{1,96} = 10.50$, P = 0.002) and liver $\delta^{15}N$ (A = 6.73, I = 7.82; $F_{1,96} = 50.01$, P < 0.0001) values (Figs. 4.1 and 4.3). In liver $\delta^{13}C$ values there was a significant status*year interaction ($F_{1,96} = 6.47$, P = 0.02); there was no difference between arriving and incubating individuals in 2004 (A = -25.25, I = -25.28; P = 0.88), while in 2005 there was a significant difference (A = -25.75, I = -24.94; P = 0.0008). Snow geese enriched liver $\delta^{15}N$ (A = 6.57, I = 7.90; $F_{1,94} = 114.38$, P < 0.0001) values from arrival to early incubation; liver $\delta^{13}C$ (A = -22.17, I = -22.41; $F_{1,94} = 62.19$, P < 0.0001) values also enriched, while controlling for significant effects of year ($F_{1,94} = 7.52$, P = 0.007) (Figs. 4.2 and 4.3). In breast $\delta^{15}N$ values there was a significant status*year interaction ($F_{1,94} = 5.31$, P = 0.02); there was enrichment between arriving and incubating individuals in 2004 (A = 6.46, I = 6.97; P = 0.002), while in 2005 there was no difference (A = 6.88, I = 6.86; P = 0.91). There were no differences between arrival and incubation in snow goose abdominal fat $\delta^{13}C$ or breast $\delta^{13}C$ values (all $P \geq 0.11$) (Figs. 4.2 and 4.3).

Likewise, there were differences in $\delta^{13}C$ isotopic signatures of egg components between arrival and early incubation. In general, egg constituents enriched and because local foods are depleted in isotope values compared to goose tissues, enrichment of egg constituents from arrival to incubation indicated increased reliance on endogenous reserves once reaching the colony. Specifically, yolk lipid $\delta^{13}C$ signatures, while controlling for an effect of species (species effect, Wilks' $\lambda = 0.95$, $F_{1,166} = 8.16$, P = 0.005), significantly enriched from arrival to incubation (A = -28.92, I = -28.52; status effect, Wilks' $\lambda = 0.94$, $F_{1,166} = 10.71$, P = 0.001). Yolk protein $\delta^{13}C$ signatures, while controlling for an effect of species (species effect, Wilks' $\lambda = 0.77$, $F_{1,166} = 48.92$, P < 0.0001), also enriched from arrival to incubating birds (A = -24.95, I = -24.47; status effect, Wilks' $\lambda = 0.78$, $F_{1,166} = 46.05$, P < 0.0001). In albumen $\delta^{13}C$ values, after controlling for species effect (species effect, Wilks' $\lambda = 0.64$, $F_{1,103} = 58.43$, P < 0.0001), there was a

significant status*year interaction (status*year interaction, Wilks' $\lambda = 0.92$, $F_{1,103} = 8.40$, P = 0.004) suggesting no differences between arriving and incubating individuals in 2004 (A = -24.85, I = -24.58; P = 0.18) or 2005 (A = -24.24, I = -25.56; P = 0.17), but only annual differences in arrival bird albumen $\delta^{13}C$ values (2004 = -24.85 and 2005 = -24.24; P = 0.005). There were no differences in $\delta^{15}N$ isotopic signatures of yolk protein (A = 6.95, I = 7.08; status effect, Wilks' $\lambda = 0.99$, $F_{1,167} = 0.86$, P = 0.35) or albumen (A = 6.39, I = 6.68; status effect, Wilks' $\lambda = 0.98$, $F_{1,106} = 2.04$, P = 0.16) between arrival and early incubation birds.

Additional univariate analyses detected differences between egg constituents of arrival and early incubation birds within species (Fig. 4.3). In Ross's geese, yolk lipid $\delta^{13}C$ values, while controlling for a year effect ($F_{1,86} = 13.77$, P = 0.0004), significantly enriched (A = -29.16, I = -28.67; $F_{1,86} = 13.26$, P = 0.0005); yolk protein $\delta^{13}C$ (A = -25.21, I = -24.70; $F_{1,86} = 26.32$, P < 0.0001) values significantly enriched as well. Univariate analyses in albumen $\delta^{13}C$ suggested isotopic differences between status and year (status*year interaction, $F_{1,58} = 9.73$, P = 0.003) such that in 2004 birds enriched albumen (A = -25.33, I = -24.92; P = 0.02), but in 2005 birds depleted albumen (A = -24.47, I = -24.83; P = 0.04) from arrival to incubation. No changes occurred in yolk protein $\delta^{15}N$ or albumen $\delta^{15}N$ values (all $P \geq 0.89$) (Fig. 4.3). Consistent with egg isotopic changes, Ross's geese increased endogenous contributions by 15% (86% capital breeding) and 19% (75% capital breeding) in yolk protein and 36% (85% capital breeding) and 12% (95% capital breeding) in yolk lipid after birds arrived at the colony, in both years respectively (Table 4.4). Inferences about endogenous inputs in albumen also agreed with egg isotopic trends; there was a 20% increase (54% capital breeding) and 15% decrease (52% capital breeding) in endogenous inputs to albumen once birds arrived at the colony in 2004 and 2005, respectively (Table 4.4).

In snow geese, there were no changes in albumen $\delta^{13}C$ or yolk protein $\delta^{15}N$ values (all $P \geq 0.11$) after birds arrived onto the colony (Fig. 4.3). Further, yolk lipid $\delta^{13}C$ values, while controlling for a year effect ($F_{1,81} = 11.96$, P = 0.0009) did not change after birds arrived onto the colony (A = -28.72, I = -28.50; $F_{1,81} = 2.70$, P = 0.10). Yet, there was enrichment in albumen $\delta^{15}N$ (A = 6.04, I = 6.79; $F_{1,48} = 4.88$, P = 0.03) and yolk protein $\delta^{13}C$ (A = -24.68, I = -24.25; $F_{1,81} = 21.96$, P < 0.0001) signatures, while controlling for a year effect ($F_{1,81} = 10.52$, P = 0.002) (Fig. 4.3). In accordance with egg isotopic changes, snow geese increased endogenous inputs by 14% (69% capital breeding) and 11% (62% capital breeding) in yolk protein in each year (Table

4.5). However, in 2004, snow geese increased endogenous inputs by 4% (50% capital breeding) and then, in 2005, decreased endogenous inputs by 3% (48% capital breeding) in albumen after arriving at the colony (Table 4.5). Yolk lipid $\delta^{13}C$ values remained unchanged as did breeding strategy estimates for yolk lipid in each year (Table 4.5). Overall, enrichment in isotopic signatures of tissues and egg components reflects increased reliance on endogenous reserves once reaching the breeding colony.

4.3.4 Use of reserves and laying sequence

Reliance on endogenous nutrients by Ross's geese changed between first (F) and last (L) eggs within a clutch in each year (Tables 4.2 and 4.4). In 2004, exogenous contributions increased within yolk protein by 9% (77% capital breeding) in the last-laid egg. Likewise, yolk protein $\delta^{13}C$ (F = -24.63, L = -24.91; paired t = 3.46, P = 0.002) values were significantly depleted in last eggs, though there was no difference in yolk protein $\delta^{15}N$ values (F = 6.96, L = 7.23; paired t = -1.92, P = 0.07). Conversely, there were no differences in endogenous contributions in yolk lipid or albumen as laying progressed by Ross's geese. There were similar albumen $\delta^{13}C$ (F = -24.91, L = -24.94; paired t = 0.21, P = 0.83) signatures, though yolk lipid $\delta^{13}C$ signatures (F = -28.97, L = -28.60; paired t = -3.21, P = 0.004) and albumen $\delta^{15}N$ (F = 6.52, L = 7.71; paired t = -7.33, P <0.0001) of last eggs enriched suggesting increased endogenous inputs. In 2005, endogenous contributions to yolk protein were similar among first and last-laid eggs. Likewise, there were no differences in yolk protein $\delta^{13}C$ (F = -24.77, L = -24.80; paired t = 0.75, P = 0.46) values, but yolk protein $\delta^{15}N$ values (F = 7.13, L = 7.54; paired t = -2.86, P = 0.01) were enriched. However, there was a 14% (66% capital breeding) increase in endogenous inputs from first to last-laid eggs in albumen. As a result, albumen $\delta^{15}N$ (F = 6.64, L = 8.24; paired t = -6.75, P <0.0001) signatures of last eggs were enriched, though albumen $\delta^{13}C$ (F = -24.83, L = -24.60; paired t = -1.56, P = 0.13) was similar. Finally, endogenous inputs by Ross's geese to yolk lipid declined by 7% (88% capital breeding) from first to last-laid eggs, though enriched yolk lipid $\delta^{13}C$ (E = -28.35, L = -27.86; paired t = -3.22, P = 0.004) signatures of last-laid eggs suggested otherwise.

Snow geese displayed consistent strategies in both years (Tables 4.2 and 4.5). In each year, endogenous inputs increased by 6% (56% capital breeding) and 12% (60% capital breeding) from first to last-laid eggs in albumen. Accordingly, in both years, albumen $\delta^{15}N$ (2004: F = 6.96, L = 7.65; paired t = -3.08, P =0.005 and 2005: F = 6.59, L = 7.73; paired t = -

7.39, P = 0.001) and albumen $\delta^{13}C$ (2005: F = -24.28, L = -23.88; paired t = -7.39, P <0.0001) signatures of last-laid eggs enriched, although there was no change in 2004 albumen $\delta^{13}C$ (F = -24.24, L = -24.07; paired t = -1.20, P = 0.24) values. There were also 11% (97% capital breeding) and 22% (99% capital breeding) increases in endogenous inputs to yolk lipid from first to last-laid eggs within a clutch in each year, respectively. Consistent with increased endogenous input, yolk lipid $\delta^{13}C$ (F = -28.79, L = -27.15; paired t = -4.18, P = 0.0006) values enriched in 2005, yet did not change in 2004 (F = -28.22, L = -28.00; paired t = -1.31, P = 0.20). Finally, there were no differences in endogenous contributions to yolk protein over the laying sequence which was supported by similar yolk protein $\delta^{15}N$ and $\delta^{13}C$ (all $P \geq 0.06$) values, though, in 2005, yolk protein $\delta^{15}N$ (F = 7.03, L = 7.26; paired t = -2.49, P = 0.02) values enriched. Overall, my results indicate an increase in endogenous inputs through the laying sequence, though depending on the year strategies may change (Tables 4.4 and 4.5).

4.3.5 Body mass and nutrient reserve dynamics during egg formation

Both species used significant amounts of endogenous reserves during breeding. There was rapid weight loss between arriving and early incubation females (Table 4.6). Early incubation female body weight averaged 72% and 77% of arriving females in Ross's and snow, respectively. Much of this was due to loss of ovarian and oviducal tissues as eggs were laid. Total somatic protein (i.e., breast, bone-free leg, gizzard, and liver) decreased by 22% and 17% from arrival to early incubation in Ross's and snow geese, respectively (Table 4.6). Breast muscles of early incubation birds were 24% and 18% lighter than those of arriving Ross's and snow geese, respectively (Table 4.6, Figs. 4.1 and 4.2). There were also rapid declines in gizzard and liver mass between arrival and early-incubation; thereafter, few changes occurred consistent with reduced feeding after birds arrive at the colony (Table 4.6, Figs. 4.1 and 4.2). Abdominal fat was also depleted rapidly between arrival and early incubation females; early incubation birds averaged 67% and 68% of that of arriving birds abdominal fat reserves in Ross's and snow geese, respectively (Table 4.6, Figs. 4.1 and 4.2). These results indicate considerable feeding before arriving onto the breeding colony and then a switch to strong reliance on stored reserves throughout clutch formation because of reduced food intake (Table 4.6, Figs. 4.1 and 4.2).

4.4 DISCUSSION

Arctic breeding geese were considered the flagships of capital breeding (Ryder 1970, Ankney and MacInnes 1978, Drent and Daan 1981) until more recent studies (Budeau et al. 1991, Choinière and Gauthier 1995) including some that relied on isotopic methods (Gauthier et al. 2003, Schmutz et al. 2006) challenged this view. For example, greater snow, brent (*Branta bernicula*), and emperor (*Anser acanagicus*) geese were inferred to use exogenous sources for most (≥45%) of egg nutrient synthesis (Gauthier et al. 2003, Schmutz et al. 2006). My findings suggest that Ross's and snow geese were largely capital breeders during egg production. I believe these colonial species, that nest at higher densities than greater snow geese, brent, and emperor geese, are largely capital breeders after arrival because they initiate RFG during late spring migration and thus, have short time lags (≤ 3d) between arrival and nest initiation (Raveling 1978, Bon 1997, Gloutney et al. 2001), and face greater competition for depleted food resources on the nesting colony (Alisauskas and Ankney 1992, Gloutney et al. 2001). The short time lags between arrival and nesting would prevent full exploitation of breeding ground forage for clutch formation. Even if this prenesting interval on nesting territories was increased, there is little quality vegetation that remains for consumption at the Karrak Lake colony since population growth has accelerated devegetation of preferred goose foods there (Gloutney et al. 2001).

I suspect that interspecific differences in breeding phenology are more important than differences in body size as explanations for interspecific differences in breeding strategies for clutch formation (Ely et al. 2007). For instance, large-bodied greater snow geese, which arrive and feed for ~ 14 days on breeding areas before initiating nests, were inferred by Gauthier et al. (2003) to be mainly income breeders. Moreover, white-winged scoters, which are large-bodied sea ducks, showed no reliance on reserves for egg production despite feeding on site for ~30 days before commencing nesting at Redberry Lake, SK (Dobush 1986). Nonetheless, body size may still be important if time lags are similar. For example, emperor geese, which are 50% larger than sympatric nesting brent geese were slightly greater capital breeders; both of these species fed for ~ 14 days on breeding areas before initiating nests (Schmutz et al. 2006).

More consistent with the migratory schedule hypothesis than the body size hypothesis, Ross's geese were greater capital breeders than snow geese. Ankney (1984) suggested that smaller species could allocate more endogenous reserves into eggs given increased metabolic and maintenance costs with smaller size. Perhaps this is why Ross's geese have a faster egg-

laying rate (1.2 versus 1.4 d); egg synthesis should be more rapid and suffer fewer rate-limiting effects of reduced or unpredictable exogenous nutrient supply when instead supplied by a steady flow of nutrients from nutrient reserves that have been stored to full capacity (Alisauskas and Ankney 1994, Ryder and Alisauskas 1995, Mowbray et al. 2000). The smaller size of Ross's geese permits a shortened breeding cycle, because of more rapid approach of adult size and capability of flight by young, compared to snow geese. This enables later arrival and nesting without necessarily later fledging by Ross's geese. By contrast, snow geese may use fewer endogenous reserves for eggs, when compared to Ross's geese, because they have more opportunity to exploit forage on penultimate migratory stops and breeding grounds for clutch formation as their spring migration is more protracted relative to Ross's geese, based on departure dates from prairie Canada and arrival dates at arctic nesting grounds (Dzubin 1965, Ryder and Alisauskas 1995). Klaassen et al. (2003) surmised that larger birds require longer refueling times during migration as larger wings require more energy for flight (Rayner 1988). Snow geese also have robust bill morphology, which permits greater exploitation of below-ground plants and stem bases during late spring migration in the arctic (Ely et al. 2007). In accordance with speculated timing of forage acquisition, Gloutney et al. (1999), in an experimental study, documented that snow geese consumed more corn than Ross's geese during the egg laying period. Thus, larger species which require a longer breeding season may be predisposed to allocating more exogenous nutrients into eggs while saving capital for incubation (Alisauskas and Ankney 1992a, Klaassen et al. 2006).

There was also evidence of subtle but significant differences in isotopic signals of somatic tissues between species. Consistent with corn consumption during spring migration through agricultural lands, snow goose breast $\delta^{15}N$ and $\delta^{13}C$ values were enriched compared to Ross's geese (Alisauskas and Ankney 1992b, Alisauskas and Hobson 1993). I suspect that depleted Ross's geese breast values resulted from foraging on natural green vegetation (graminoid leaves and shoots) and/or emerging agricultural crops (wheat) during early spring migration as their migration is later than snow geese (Alisauskas and Hobson 1993, Ryder and Alisauskas 1995, Bon 1997). Because breast muscles have a relatively slow turnover rate (half life 12.4 d), isotopic signatures of foods consumed during spring migration are still evident on the breeding grounds (Hobson and Clark 1992, Gauthier et al. 2003). Snow goose liver $\delta^{13}C$ values were also enriched compared to Ross's geese, which is likely related to drawing on

enriched endogenous protein reserves at the colony to fuel metabolism. However, there was correspondence between species in liver isotope ratios during arrival (all $P \geq 0.20$ except liver $\delta^{13}C$ in 2005 $P = 0.0008$) implying that birds were eating similar forage at penultimate migratory stops given that liver reflects recently consumed nutrients used during intermediary metabolism (half life turnover 2.6 d; Hobson and Clark 1992). There were also no differences in abdominal fat $\delta^{13}C$ values since birds feed intensively for up to a month on similar waste grains on the Canadian prairies before they depart to the breeding grounds (Alisauskas and Ankney 1992b, Bon 1997). For example, Ross's geese can store ~290 g of fat reserves at this time (Bon 1997).

Differences in breeding strategies were evident among years within yolk protein and yolk lipid. Because there were little annual differences in tissue isotopic values, Ross's and snow geese displayed consistent annual nutrient acquisition and thus, plasticity in breeding strategies. In 2004 (i.e., a year with nesting phenology close to average), both species increased endogenous inputs into yolk protein when compared to 2005 (i.e., a year with nesting phenology earlier than average), albeit snow goose somatic contribution was 13% to 16% less. Thus, both species reduced their somatic protein contribution into eggs in the early year; a pattern consistent with increased food availability which, in turn allows assimilation of forage protein into developing follicles. Both species have been documented to acquire protein from green vegetation on migratory stops before arriving onto the colony as they follow the spring development of green vegetation (Drent et al. 1978, Wypkema and Ankney 1979, Bon 1997). Snow goose liver $\delta^{13}C$ values were significantly depleted in 2005 further suggesting assimilation of local vegetation. In contrast, Ross's geese yolk protein $\delta^{13}C$ values were similar among years, though it remains uncertain why, because there was a significant decrease in endogenous contribution to yolk protein in 2005. Additionally, there was no difference in breast isotope values among years or changes in yolk protein $\delta^{15}N$ signatures which suggests consistency in endogenous protein (nitrogen) allocation. Alternatively, Bauer et al. (2008) showed that Pink-footed geese (*Anser brachyrhynchus*) used locally accumulated temperatures to increase their rate of spring migration to colonies when it was warmer and subsequently predicted geese to skip their northern most staging area during early springs to head more expeditiously for breeding colonies. This would suggest less opportunity to exploit green vegetation for protein in early years. Ross's geese actually decreased endogenous inputs to yolk lipid in the normal year, while snow geese increased somatic lipid contribution. Specifically, snow geese used 22% less somatic fat in the

year with early phenology than Ross's geese. Perhaps this disparity in somatic lipid resulted from differing migratory schedules as snow geese have more time to exploit migratory forage for clutch lipid in early years and ensure adequate lipid reserves for incubation.

Conceivably, variation in nutrient allocation strategies (i.e., in yolk lipid and yolk protein) may only occur in species with short time-lags between arrival and nesting as they are predisposed to be greater capital breeders. For example, Gauthier et al. (2003) found little annual variation in endogenous contribution to eggs in greater snow geese which feed on nesting areas for ~14 d before initiating nests. However, inclement weather (snow cover) during this time period could prohibit food acquisition and force geese to utilize more endogenous reserves and thus create variation in allocation strategies. My results suggest consistency in albumen strategies among years and between species (~50% capital and 50% income strategies). I think that, given the rapid synthesis of albumen (2.5 hrs) (Hobson 1995), amino acid demand during development requires a mixed strategy to circumvent rate-limiting effects of interrupted supply during this time. While there were similar strategies for supplying albumen between species and years, there was increased variance in albumen strategies of first laid eggs compared to last laid eggs implying differences in female allocation strategies during the laying sequence (Tables 4.4 and 4.5). Gauthier et al. (2003) inferred that greater snow geese allocated ~74% local food plants to albumen synthesis. In my study, bryophytes were an unexpectedly important source of protein for albumen formation. Gloutney et al. (2001) documented comparable consumption amounts of moss by both species during egg-laying at Karrak Lake. Alternatively, because amino acid content of yolk protein and albumen is similar (Murphy 1994) differences in perceived allocation may be due to differing metabolic pathways and respective isotopic discrimination.

4.4.1 Income signals from penultimate staging areas

Ross's and snow geese breeding at Karrak Lake commence rapid follicle growth before reaching the breeding colony (Raveling 1979, Bon 1997). Thus, it is possible that nutrient allocation to developing ova can be from somatic reserves and/or staging area foods. My results of depleted liver $\delta^{13}C$ and $\delta^{15}N$ values in arriving geese indicate consumption of forage on migratory stops before arrival onto the breeding colony. It is known that Ross's and snow geese experience hyperphagia on staging areas south of Karrak Lake to meet demands of migration and recrudescence of reproductive organs (Bon 1997). Wypkema and Ankney (1979) documented

that female snow geese leaving a spring staging area maintained fat reserves, gained ~14 g protein (equivalent to the protein in one egg), and increased overall body mass 240 g. This tactic of storing reserves locally for breeding has also been documented in lesser scaup, which arrive onto breeding areas and accumulate protein reserves, while maintaining lipid reserves before egg laying (Afton and Ankney et al. 1991). By contrast, the general isotopic enrichment of tissues once on the breeding colony, with simultaneous reductions in food intake and rapid declines in mass of those same tissues suggested preferential mobilization of somatic tissue for metabolism and egg synthesis (Figs. 4.1 and 4.2). For example, enriched liver $\delta^{13}C$ and $\delta^{15}N$ values of geese at the colony implied that differential use of lighter isotopes as protein reserves were used to meet nutritional and metabolic costs of egg synthesis (Hobson et al. 1993). Indeed, egg constituents generally enriched from arrival to early incubation (i.e., developing follicles to first-laid egg components) demonstrating increases in use of endogenous reserves for egg formation after birds reached the breeding colony. Thus, implying these arctic-breeding geese are predominantly capital breeders with most nutrients supplied to eggs coming from reserves, though income signals were present in developing follicles and first-laid eggs they were indicative of plants assimilated from staging areas and not at the colony.

I think that evidence of local income signals are expected in eggs of these arctic geese. Local income signals are residual staging area income signals within yolk protein and yolk lipid because yolk is synthesized over a 12 day period (RFG is 12 days) and yolk of first-laid eggs is almost completely formed when birds arrive at the colony (~27 g w/w; Traylor unpubl. data) (Alisauskas and Ankney 1992b, Slattery and Alisauskas 1995). Moreover, Hobson (1995) suggested that a new isotopic equilibrium in yolk is reached 8 days following a diet switch. Because breeding strategies and concomitant enrichment of egg constituents displayed considerable shifts in such a short amount of time (3 to 5 d period from arrival to nest initiation; Raveling 1979), these findings further suggested that endogenous reserves were the predominant precursor for egg synthesis when birds arrived at the colony (Hobson and Clark 1992). Consequently, even in last-laid egg components exogenous signals were still present, though results suggested a general attenuation of the exogenous signal. However, albumen synthesis remained a combination of endogenous and exogenous sources (see above). The increase in C:N ratio (see below) of albumen from arrival to early incubation ($A = 3.73$, $I = 3.79$; $P = 0.02$) suggested a decrease in quality of protein being partitioned into this constituent; this was consistent with the

idea that assimilated nutrients from forage at the colony was marginal or that birds reallocated protein from another lower quality source to satisfy the high protein demand during albumen synthesis (Raveling 1979, Ankney 1984). The C:N ratio is an index of protein quality and/or lipid content such that lower numbers indicate greater protein quality or lower lipid content (Robbins et al. 2005, Post et al. 2006). Finally, I suggest that attention restricted solely to post-laying birds would have suggested that birds displayed a largely income-biased strategy, at variance with my conclusions for a greater reliance on capital resources.

4.4.2 Laying sequence effects

Ross's and snow geese displayed different breeding strategies as clutch production progressed (i.e., from first to last-laid eggs). Snow geese consistently increased endogenous inputs in albumen and yolk lipid further suggesting increasing dependence upon endogenous reserves as egg-laying progressed. Large body size of snow geese permitted storage of absolutely more reserves than Ross's geese, thereby permitting increased endogenous inputs throughout the laying sequence by snow geese. Earlier arrival and nesting by snow geese forces greater use of snow-free rocky habitat in upland areas of the colony, whereas the later arrival of Ross's geese permits occupancy of lowland, better-vegetated areas previously unavailable to many snow geese, because of snow cover. Yet, upland areas have less forage than lowland areas (Ryder and Alisauskas 1995, Gloutney et al. 2001, Alisauskas et al. 2006a), so that snow geese restricted to such upland areas had to increase reserve use as laying progressed.

In contrast to the less variable strategy observed in snow geese, Ross's geese displayed flexibility in strategies either by increasing endogenous or exogenous inputs in all constituents. Ross's geese initially partitioned large amounts of endogenous reserves into eggs as is predicted under some circumstances for smaller-bodied species (Ankney 1984). Generally, their less efficient metabolism, due to smaller size, was predicted to predispose them to exploiting exogenous food sources as egg-laying progressed, yet strategies of nutrient supply to eggs were different in each year throughout the laying sequence. For instance, in 2004 when nesting phenology was close to average, Ross's geese increased exogenous inputs into yolk protein while in the early year of 2005, there was no change. In 2004, there was a significant concurrent increase in C:N ratio of yolk protein ($E = 3.50$, $L = 3.63$, $P=0.005$) suggesting a decline in protein quality as females supplied more nutrient directly from local foods into last-laid eggs. As

laying progressed in the year with normal nesting phenology, female Ross's geese may have foraged more to conserve somatic protein reserves as protein can be a more limiting egg nutrient than fat (Meijer and Drent 1999, Gauthier et al. 2003). However, in 2005 the C:N ratio (E = 3.55, L = 3.67, P = 0.003) also indicated a decrease in protein quality when there was no change in breeding strategies. Conceivably, Ross's geese may have allocated protein from another source of lesser quality such as liver or gizzard (Table 4.2) (Raveling 1979, Ankney 1984).

Overall, these results are consistent with evidence that snow geese partition more staging area foods into first-laid egg components and when on the breeding colony they increasingly allocate more somatic protein and fat to clutch formation than Ross's geese. I suspect that a short time lag between arrival and nesting, with concurrent reductions in feeding opportunities, require increased endogenous inputs as laying progresses. Nevertheless, smaller body size of Ross's geese demands a more flexible strategy as laying progresses in response to prevailing ambient conditions in feeding opportunities. Though individual snow goose females significantly increased endogenous contributions as laying progressed, Ross's geese still, overall, contributed proportionally more endogenous inputs into clutch formation than snow geese in each year.

4.4.3 Body and tissue mass dynamics

Enlarged organs of digestion (gizzard) and intermediary metabolism (liver) of females collected at arrival suggested hyperphagia on staging areas south of the breeding colony to meet demands of migration and recrudescence of reproductive organs, also consistent with my inference about the important role of local capital for egg formation (Ankney 1977, Wypkema and Ankney 1979, Bon 1997). In addition to Gloutney et al. (2001), my results are strongly consistent with reduced food intake during egg formation (Ankney 1977, Ankney and MacInnes 1978) (Figs. 4.1 and 4.2). Furthermore, consistent with (i) temporal changes in breeding strategies (from developing follicles to last-laid eggs in a clutch), and (ii) isotopic signatures of tissues and egg components suggesting endogenous inputs to clutch formation, geese experienced significant and concurrent declines in body and tissue masses not only from pre- to post-laying but until hatch (Figs. 4.1 and 4.2). This demonstrated that endogenous nutrients are not only the main substrate for clutch formation but also for incubation (Ankney 1977, Ankney and MacInnes 1978).

Even if limited foraging occurred on the colony, it would not have be enough to satisfy egg production. For example, both species initiate RFG before arrival to the colony, allowing

exploitation of available vegetation, and direct allocation of some exogenous nutrients directly into developing ovaries thereby supplementing the supply from endogenous reserves while on staging areas. Ross's and snow geese, on average, produce clutches that contain the equivalent of ~18.8 g and 26.1 g of albumen, 22.0 g and 31.3 g of yolk protein, and 40.1 g and 54.1 g of yolk lipid, respectively (dry weight for average clutch size, Slattery and Alisauskas 1995). However, each species respectively arrived on the nesting colony with 28.3% (5.3 g) and 23.7% (6.2 g) of albumen (oviducal eggs), 49.2% (10.8 g) and 40.0% (12.6 g) yolk protein, and 49.2% (19.7 g) and 40.0% (21.7 g) of yolk lipid required for clutch formation within their developing follicles, respectively (Traylor unpubl. data). Consequently, an additional 45.1 g (13.5 g albumen, 11.2 g yolk protein, and 20.4 g yolk lipid) and 71.2 g (19.9 g albumen, 18.8 g yolk protein, and 32.5 g yolk lipid) of egg nutrients remain to be supplied to satisfy clutch completion after arrival, respectively. However, Ross's and snow geese only assimilate 4.3 g and 3.4 g daily based on daily dry matter intake of 12.4 g and 9.6 g for Ross's and snow geese with a dry matter digestibility of 35% (Manseau and Gauthier 1993, Gloutney et al. 2001). So, during the seven days between arrival and clutch completion Ross's and snow geese likely assimilated only 30.4 g and 23.5 g, respectively; most of this may be used to support daily metabolism and consequently, wouldn't completely satisfy the residual quantities required for clutch completion. Conversely, during this same time period Ross's and snow geese lost 93.1 g (59.0 g breast, 17.1 g liver, and 21.2 g gizzard) and 113.9 g (67.0 g breast, 25.8 g liver, and 37.6 g gizzard) of total protein and 19.1 g and 20.7 g of abdominal fat, respectively. Abdominal fat constitutes about 16.7% of total body fat (Bon 1997) so that decline in total body fat could have been 120 g if declines were proportional. In total, Ross's and snow geese each lost aggregate masses of 206.9 g and 162.2 g, respectively, of protein and fat from somatic tissue during this time period, while producing respective clutches with masses of 302.7 g and 424.8 g, fresh weight including shell. Accordingly, these birds had adequate quantities of protein and lipid reserves to satisfy clutch requirements with any excess available to meet maintenance requirements (Meijer and Drent 1999). Thus, my findings about mass changes of organs and depots concur with my findings from isotope analysis that most nutrients used for clutch formation arose from endogenous reserves and foods from penultimate staging areas, while further declines in somatic protein and lipid occurred during incubation (Figs. 4.1 and 4.2). Ross's geese partitioned proportionally more

reserves into eggs than snow geese and experienced greater absolute mass loss consistent with Ankney's (1984) predictions about the influence of interspecific differences in body size.

Finally, variation in allocation strategies for clutch formation along with interspecific differences in body size dictated differential patterns in incubation metabolism. Snow geese relied more on reserves for incubation based on enrichment of tissue isotopic values between early- and mid-incubation birds (Fig. 4.2). On the other hand, liver and abdominal fat $\delta^{13}C$ values of Ross's geese did not enrich from early- to mid-incubation. Thus, suggesting that Ross's geese assimilated local food plants with concurrent use of reserves to satisfy nutritional demands of incubation (Fig. 4.1). Smaller-body size of Ross's geese limits the amount of reserves they can carry and renders their metabolism relatively inefficient compared to snow geese. Consequently, Ross's geese forage during incubation so they do not completely exhaust reserves, which could cause nest abandonment or in extreme cases death.

In sum, arctic breeding birds face greater time constraints than those that nest at lower latitudes because of the shortness of snow-free periods with access to arctic foods. Capital breeding is a strategy that decouples nutrient requirements of egg formation from food availability and thus should be more prevalent among arctic-breeding herbivorous birds. However, various life history characteristics such as timing and location of initiation of RFG, migration schedule, and body size can "fine-tune" reliance upon capital breeding (Drent et al. 2006, Ely et al. 2007). Overall, both Ross's and snow geese showed a predominance of capital breeding for egg formation. There was very limited opportunity for income breeding on the colony because of an absence of food there, but some apparent income allocation to eggs occurred from foods consumed at arctic staging areas before arrival at the colony. Some reliance on income nutrients promotes flexibility for nutrient supply to developing ovaries as it allows birds to compensate for unpredictable weather events in highly constrained environments. Birds facing time constraints between arrival on their nesting colonies and following by immediate nesting benefit from feeding opportunities available at sites other than the colony itself where foods may have been depleted by long-term nesting. Consequently, my results confirm the importance of northern migratory stops, particularly for protein acquisition (Wypkema and Ankney 1979). Last, Ross's geese made greater proportional use of endogenous inputs into clutch formation than snow geese; however, constraints of small body size (i.e., higher metabolism, smaller nutrient reserves) cause Ross's geese to forage and use endogenous reserves

during incubation, while snow geese rely on endogenous reserves (Gloutney et al. 2001). Ultimately, the ability of Ross's geese to exploit marginal quality vegetation in conjunction with somatic reserves to offset energetic demands of incubation may explain why they do not display large decreases in nest success with delays in breeding as do snow geese (Raveling 1978).

Table 4.1. Mean isotopic signatures ($\delta^{13}C$ and $\delta^{15}N$ in ‰), C:N ratio, and sample size of somatic tissues (breast, abdominal fat, liver) and eggs (yolk protein, albumen, yolk-lipid) for arriving Ross's and snow geese in 2004 and 2004, respectively.

		Ross's Geese				Snow Geese			
Year	**Tissue**	**$\delta^{13}C$[a]**	**$\delta^{15}N$[b]**	**C:N[c]**	***n*[d]**	**$\delta^{13}C$**	**$\delta^{15}N$**	**C:N**	***n***
2004	Breast muscle	-24.46 ± 1.18	6.39 ± 0.46	3.35	25	-22.06 ± 0.72	6.46 ± 0.45	3.33	25
	Abdominal fat	-26.36 ± 1.38		1412.65	25	-25.14 ± 1.22		2182.60	25
	Liver	-25.25 ± 1.18	6.61 ± 0.72	4.30	25	-24.97 ± 0.46	6.56 ± 0.61	4.89	25
	Yolk protein	-25.37 ± 0.52	6.93 ± 0.86	3.87	18	-24.52 ± 0.53	6.87 ± 1.01	3.96	21
	Albumen[e]	-25.33 ± 0.61	6.11 ± 0.72	3.74	8	-24.28 ± 0.26	6.02 ± 0.53	3.76	5
	Yolk lipid	-29.33 ± 0.58		323.25	21	-28.54 ± 0.59		326.42	21
2005	Breast muscle	-23.68 ± 1.03	6.71 ± 0.53	3.33	29	-22.30 ± 0.83	6.88 ± 0.62	3.31	27
	Abdominal fat	-26.29 ± 1.28		2317.22	29	-25.30 ± 1.37		3292.47	27
	Liver	-25.75 ± 0.54	6.83 ± 0.91	4.95	29	-25.21 ± 0.58	6.57 ± 0.53	4.96	27
	Yolk protein	-25.11 ± 0.51	7.17 ± 1.09	3.86	26	-24.87 ± 0.35	6.75 ± 0.67	3.92	19
	Albumen	-24.47 ± 0.53	6.98 ± 0.76	3.70	8	-24.31 ± 0.64	6.09 ± 0.13	3.71	2
	Yolk Lipid	-28.96 ± 0.51		782.82	26	-28.91 ± 0.60		298.97	19

[a] Mean $\delta^{13}C$ ± standard deviation
[b] Mean $\delta^{15}N$ ± standard deviation
[c] Mean ratio of %C divided by %N in the sample; indicator of protein quality (lower numbers indicate greater protein quality) or lipid content (higher numbers indicate greater lipid content) (Robbins et al. 2005; Post et al. 2006)
[d] Sample size
[e] Albumen was only present within oviducal eggs of arriving females

Table 4.2. Mean isotopic signatures ($\delta^{13}C$ and $\delta^{15}N$ in ‰), C:N ratio, and sample size of somatic tissues (breast, abdominal fat, liver) first, and last-laid eggs within a clutch (yolk protein, albumen, yolk-lipid) for early-incubating (post-laying) Ross's and snow geese in 2004 and 2005, respectively.

		Ross's Geese				Snow Geese			
Year	**Tissue**	**$\delta^{13}C$[a]**	**$\delta^{15}N$[b]**	**C:N[c]**	***n*[d]**	**$\delta^{13}C$**	**$\delta^{15}N$**	**C:N**	***n***
2004	Breast muscle	-24.06 ± 0.84	6.35 ± 0.39	3.34	22	-22.49 ± 0.88	6.97 ± 0.57	3.38	23
	Abdominal fat	-25.64 ± 1.41		2320.54	22	-24.74 ± 1.05		1881.92	23
	Liver	-25.28 ± 0.50	7.63 ± 0.50	4.29	22	-24.06 ± 0.56	7.98 ± 0.65	4.17	23
	First eggs								
	Yolk protein	-24.63 ± 0.38	6.96 ± 0.82	3.50	22	-24.13 ± 0.39	7.17 ± 0.89	3.58	22
	Albumen	-24.92 ± 0.39	6.52 ± 0.89	3.78	22	-24.24 ± 0.47	6.96 ± 0.92	3.79	22
	Yolk lipid	-28.97 ± 0.55		1083.32	22	-28.22 ± 0.66		648.38	22
	Last eggs								
	Yolk protein	-24.91 ± 0.36	7.23 ± 0.85	3.63	22	-24.17 ± 0.32	7.53 ± 1.04	3.54	23
	Albumen	-24.94 ± 0.46	7.71 ± 0.89	3.80	22	-24.07 ± 0.53	7.65 ± 1.00	3.80	23
	Yolk lipid	-28.60 ± 0.62		902.88	22	-28.00 ± 0.60		966.54	23
2005	Breast muscle	-23.76 ± 0.97	6.85 ± 0.51	3.32	21	-22.38 ± 0.67	6.86 ± 0.57	3.34	20
	Abdominal fat	-25.07 ± 1.78		3719.19	21	-25.15 ± 0.86		3475.69	20
	Liver	-24.94 ± 0.84	8.01 ± 0.72	4.32	21	-24.41 ± 0.45	7.81 ± 0.66	4.49	20
	First eggs								
	Yolk protein	-24.77 ± 0.41	7.14 ± 1.06	3.55	21	-24.38 ± 0.40	7.04 ± 0.77	3.62	20
	Albumen	-24.83 ± 0.34	6.64 ± 0.93	3.78	21	-24.28 ± 0.35	6.59 ± 0.78	3.80	20
	Yolk lipid	-28.35 ± 0.83		971.26	21	-28.79 ± 0.60		646.19	20
	Last eggs								
	Yolk protein	-24.80 ± 0.46	7.54 ± 0.81	3.58	20	-24.31 ± 0.44	7.26 ± 0.75	3.71	19
	Albumen	-24.61 ± 0.78	8.24 ± 0.77	3.70	20	-23.88 ± 0.61	7.73 ± 0.94	3.80	19
	Yolk lipid	-27.86 ± 1.12		797.87	20	-28.15 ± 0.82		317.83	19

[a] Mean $\delta^{13}C$ ± standard deviation

[b] Mean $\delta^{15}N$ ± standard deviation

[c] Mean ratio of %C divided by %N in the sample; indicator of protein quality (lower numbers indicate greater protein quality) or lipid content (higher numbers indicate greater lipid content) (Fantle et al. 1999; Post et al. 2006)

[d] Sample size

Table 4.3. Mean isotopic signatures ($\delta^{13}C$ and $\delta^{15}N$ in ‰), C:N ratio, and sample size of food plants consumed by Ross's and snow geese at the Karrak Lake light goose colony, south of Queen Maud Gulf, Nunavut, Canada.

Food item	**$\delta^{13}C$[a]**	**$\delta^{15}N$[b]**	**C:N[c]**	***n*[d]**	**Tissue type**
Stellaria spp.	-27.61 ± 0.69	6.49 ± 2.04	4.82	3	Leaves
Bryophytes	-26.78 ± 0.84	2.05 ± 1.31	10.56	6	Leaves
Carex spp.	-27.36 ± 0.86	3.85 ± 1.16	5.59	11	Leaves, roots
Shrubs[e]	-28.59 ± 0.84	-0.89 ± 2.77	21.11	15	
Arctostaphylos spp.	-29.26 ± 0.68	-4.11 ± 0.80	43.85	2	Berries
Vaccinium vitus-idaea	-28.52 ± 1.13	-1.76 ± 2.20	25.63	7	Leaves, berries
Empetrum nigrum	-28.51 ± 0.24	2.00 ± 1.07	23.47	3	Leaves
Ledum decumbens	-28.38 ± 0.81	0.36 ± 3.15	11.68	3	Leaves

[a] Mean $\delta^{13}C$ ± standard deviation

[b] Mean $\delta^{15}N$ ± standard deviation

[c] Mean ratio of %C divided by %N in the sample; indicator of protein quality (lower numbers indicate greater protein quality) or lipid content (higher numbers indicate greater lipid content) (Robbins et al. 2005; Post et al. 2006). C:N ratios of shrubs are adjusted for assimilation differences of berries following Koch and Phillips (2002).

[d] Sample size

[e] Mean of all four shrubs listed

Table 4.4. Mean proportion of egg nutrients derived by Ross's geese from somatic reserves and breeding ground food plants based on isotopic composition of somatic reserves, food plants, and egg nutrients for the 1) largest developing follicle or oviducal egg of arriving females and 2) first and 3) last-laid eggs within a clutch for early incubating females in 2004 and 2005. In some cases yolk lipid estimates were inestimable as the mixture fell outside the source bounds. In these cases, expected estimates of proportional capital breeding were generated based on the relationship with varying discrimination factors (see Appendix).

		Arrival		**First Egg**		**Last Egg**	
Year	**Egg nutrients and sources**	Mean	95% CL	Mean	95% CL	Mean	95% CL
2004	Yolk protein						
	Reserves	0.71	0.67, 0.76	0.86	0.83, 0.88	0.77	0.75, 0.80
	Bryophytes	0.11	0.00, 0.24	0.06	0.00, 0.15	0.05	0.00, 0.13
	Carex spp.	0.08	0.00, 0.17	0.03	0.00, 0.06	0.08	0.00, 0.20
	Shrubs	0.05	0.00, 0.11	0.04	0.00, 0.07	0.02	0.00, 0.06
	Stellaria spp.	0.05	0.00, 0.09	0.01	0.00, 0.03	0.08	0.00, 0.12
	Albumen						
	Reserves	0.34	0.10, 0.63	0.54	0.40, 0.69	0.57	0.54, 0.62
	Bryophytes	0.41	0.03, 0.74	0.25	0.01, 0.50	0.06	0.00, 0.15
	Carex spp.	0.09	0.00, 0.21	0.07	0.00, 0.15	0.08	0.00, 0.15
	Shrubs	0.11	0.00, 0.25	0.10	0.00, 0.19	0.02	0.00, 0.06
	Stellaria spp.	0.05	0.00, 0.10	0.04	0.00, 0.07	0.26	0.19, 0.30
	Yolk lipid						
	Reserves	0.49	-	0.85	0.78, 0.91	0.85	0.77, 0.91
	Bryophytes	-	-	0.07	0.00, 0.19	0.07	0.00, 0.20
	Carex spp.	-	-	0.03	0.00, 0.09	0.03	0.00, 0.10
	Shrubs	-	-	0.02	0.00, 0.04	0.02	0.00, 0.04
	Stellaria spp.	-	-	0.03	0.00, 0.08	0.03	0.00, 0.08
2005	Yolk protein						
	Reserves	0.56	0.52, 0.61	0.75	0.70, 0.79	0.74	0.71, 0.76
	Bryophytes	0.12	0.00, 0.29	0.11	0.00, 0.25	0.06	0.00, 0.15
	Carex spp.	0.15	0.00, 0.33	0.05	0.00, 0.11	0.09	0.00, 0.22
	Shrubs	0.06	0.00, 0.15	0.07	0.00, 0.13	0.03	0.00, 0.08
	Stellaria spp.	0.10	0.00, 0.19	0.02	0.00, 0.06	0.08	0.00, 0.13
	Albumen						
	Reserves	0.67	0.59, 0.75	0.52	0.38, 0.65	0.66	0.65, 0.67
	Bryophytes	0.15	0.00, 0.31	0.25	0.01, 0.50	0.02	0.00, 0.05
	Carex spp.	0.07	0.00, 0.15	0.08	0.00, 0.17	0.03	0.00, 0.07
	Shrubs	0.07	0.00, 0.13	0.11	0.00, 0.22	0.01	0.00, 0.02
	Stellaria spp.	0.04	0.00, 0.07	0.04	0.00, 0.08	0.28	0.26, 0.30
	Yolk lipid						
	Reserves	0.83	-	0.95	0.94, 0.96	0.88	-
	Bryophytes	-	-	0.02	0.00, 0.05	-	-
	Carex spp.	-	-	0.01	0.00, 0.03	-	-
	Shrubs	-	-	0.01	0.00, 0.02	-	-
	Stellaria spp.	-	-	0.01	0.00, 0.03	-	-

Table 4.5. Mean proportion of egg nutrients derived by snow geese from somatic reserves and breeding ground food plants based on isotopic composition of somatic reserves, food plants, and egg nutrients for the 1) largest developing follicle or oviducal egg of arriving females and 2) first and 3) last-laid eggs within a clutch for early incubating females in 2004 and 2005. In some cases yolk lipid estimates were inestimable as the mixture fell outside the source bounds. In these cases, expected estimates of proportional capital breeding were generated based on the relationship with varying discrimination factors (see Appendix).

Year	Egg nutrients and sources	Arrival		First Egg		Last Egg	
		Mean	95% CL	Mean	95% CL	Mean	95% CL
2004	Yolk protein						
	Reserves	0.55	0.51, 0.59	0.69	0.66, 0.72	0.67	0.65, 0.70
	Bryophytes	0.15	0.00, 0.33	0.12	0.00, 0.28	0.08	0.00, 0.20
	Carex spp.	0.13	0.00, 0.30	0.07	0.00, 0.16	0.11	0.00, 0.27
	Shrubs	0.08	0.00, 0.17	0.08	0.00, 0.15	0.04	0.00, 0.11
	Stellaria spp.	0.09	0.00, 0.17	0.04	0.00, 0.09	0.09	0.00, 0.15
	Albumen						
	Reserves	0.46	0.36, 0.53	0.50	0.43, 0.58	0.56	0.52, 0.60
	Bryophytes	0.22	0.01, 0.54	0.18	0.01, 0.40	0.09	0.00, 0.22
	Carex spp.	0.07	0.00, 0.18	0.14	0.00, 0.30	0.14	0.00, 0.35
	Shrubs	0.21	0.00, 0.31	0.10	0.00, 0.20	0.04	0.00, 0.11
	Stellaria spp.	0.04	0.00, 0.10	0.08	0.00, 0.16	0.16	0.06, 0.24
	Yolk lipid						
	Reserves	0.88	0.84, 0.92	0.86	0.83, 0.90	0.97	0.96, 0.98
	Bryophytes	0.05	0.00, 0.13	0.05	0.00, 0.14	0.01	0.00, 0.02
	Carex spp.	0.03	0.00, 0.09	0.03	0.00, 0.10	0.01	0.00, 0.02
	Shrubs	0.02	0.00, 0.05	0.02	0.00, 0.06	0.00	0.00, 0.01
	Stellaria spp.	0.02	0.00, 0.07	0.03	0.00, 0.09	0.01	0.00, 0.02
2005	Yolk protein						
	Reserves	0.51	0.45, 0.56	0.62	0.58, 0.66	0.63	0.60, 0.66
	Bryophytes	0.19	0.00, 0.44	0.14	0.01, 0.32	0.11	0.00, 0.25
	Carex spp.	0.11	0.00, 0.25	0.10	0.00, 0.22	0.12	0.00, 0.26
	Shrubs	0.12	0.00, 0.23	0.08	0.00, 0.17	0.06	0.00, 0.14
	Stellaria spp.	0.06	0.00, 0.14	0.06	0.00, 0.12	0.08	0.00, 0.15
	Albumen						
	Reserves	0.51	0.42, 0.56	0.48	0.39, 0.56	0.60	0.57, 0.63
	Bryophytes	0.17	0.00, 0.43	0.23	0.01, 0.50	0.07	0.00, 0.17
	Carex spp.	0.05	0.00, 0.11	0.10	0.00, 0.23	0.11	0.00, 0.28
	Shrubs	0.25	0.13, 0.33	0.13	0.01, 0.25	0.04	0.00, 0.09
	Stellaria spp.	0.02	0.00, 0.06	0.06	0.00, 0.12	0.18	0.10, 0.24
	Yolk lipid						
	Reserves	0.71	0.60, 0.80	0.73	0.63, 0.81	0.99	-
	Bryophytes	0.11	0.00, 0.33	0.10	0.00, 0.30	-	-
	Carex spp.	0.07	0.00, 0.20	0.07	0.00, 0.19	-	-
	Shrubs	0.04	0.00, 0.11	0.04	0.00, 0.11	-	-
	Stellaria spp.	0.06	0.00, 0.17	0.06	0.00, 0.16	-	-

Table 4.6. Mean changes in body and tissue mass (g, wet weight) of female Ross's and snow geese throughout breeding at the Karrak Lake light goose colony, south of Queen Maud Gulf, Nunavut, Canada, for birds collected in 2004 and 2005, respectively.

	Arriving[a]			Early Incubation[b]			Mid Incubation[c]			Late incubation[d]	
Ross's Geese	Mean	95%CL	P[e]	Mean	95%CL	P[e]	Mean	95%CL	P[e]	Mean	95%CL
Body weight	1811.06	25.33	***	1301.49	28.80	***	1145.49	50.11	***	939.09	28.83
Total Protein	432.73	9.01	***	339.61	9.85	ns	322.60	17.31	***	268.24	9.97
Breast	250.89	6.17	***	191.89	6.81	ns	184.44	11.97	***	145.19	6.89
Leg	74.24	2.62	*	78.21	2.89	ns	73.91	5.08	**	65.40	2.93
Gizzard	71.12	1.74	***	49.88	1.94	ns	46.62	3.41	**	41.13	1.96
Liver	36.79	1.13	***	19.66	1.27	ns	17.77	2.23	ns	16.55	1.29
Abdominal Fat	57.02	2.98	***	37.89	3.30	**	25.34	5.82	***	6.54	3.34
n	44			43			15			42	
Snow Geese											
Body weight	2535.84	47.42	***	1948.82	53.71	***	1612.99	94.87	**	1441.28	54.92
Total Protein	668.79	15.29	***	554.89	17.61	***	473.80	29.97	***	412.41	17.41
Breast	369.53	9.46	***	302.55	10.62	***	252.02	18.75	***	210.52	10.86
Leg	126.53	5.53	**	139.42	6.22	*	125.00	10.84	ns	113.76	6.29
Gizzard	118.85	2.94	***	81.30	3.28	**	71.85	5.78	ns	67.49	3.35
Liver	53.61	1.77	***	27.78	1.97	ns	24.11	3.48	ns	22.09	2.01
Abdominal Fat	64.24	3.89	***	43.57	4.32	***	25.11	7.63	***	8.47	4.42
n	42			43			15			40	

[a] Birds collected flying onto colony with developing follicles
[b] Birds collected during early incubation, ≤ 6 d; post-laying
[c] Birds collected during mid incubation, 7-10 d
[d] Birds collected near hatch, 17-23 d
[e] Probability that adjacent columns are statistically significant different (* P< 0.05, ** P <0.01, *** P<0.001, ns indicates P>0.05)

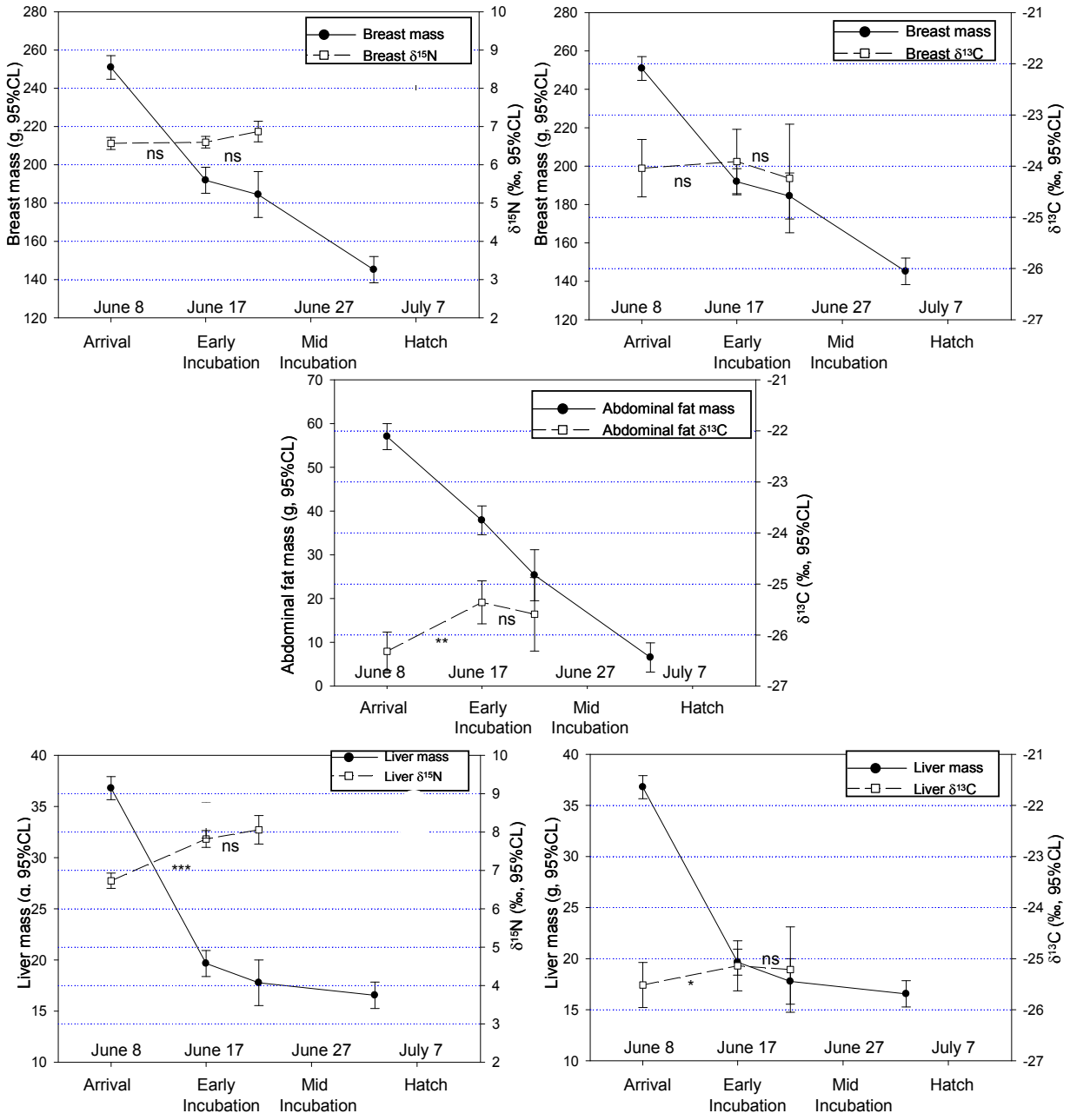


Figure 4.1. Tissue (breast, abdominal fat, and liver) mass and their isotopic values through time for Ross's geese collected at the Karrak Lake light goose colony, south of Queen Maud Gulf, Nunavut, Canada. Tissue mass values are located on the left y-axis, while stable isotope values are located on the right y-axis. Birds were collected throughout breeding, from arrival, early incubation (< 6 d), mid-incubation (7-10 d), and at hatch (17-23 d). Symbols near dashed lines indicate whether there are differences in isotopic values between successive time periods (* P< 0.05, ** P <0.01, *** P<0.001, ns indicates P>0.05).

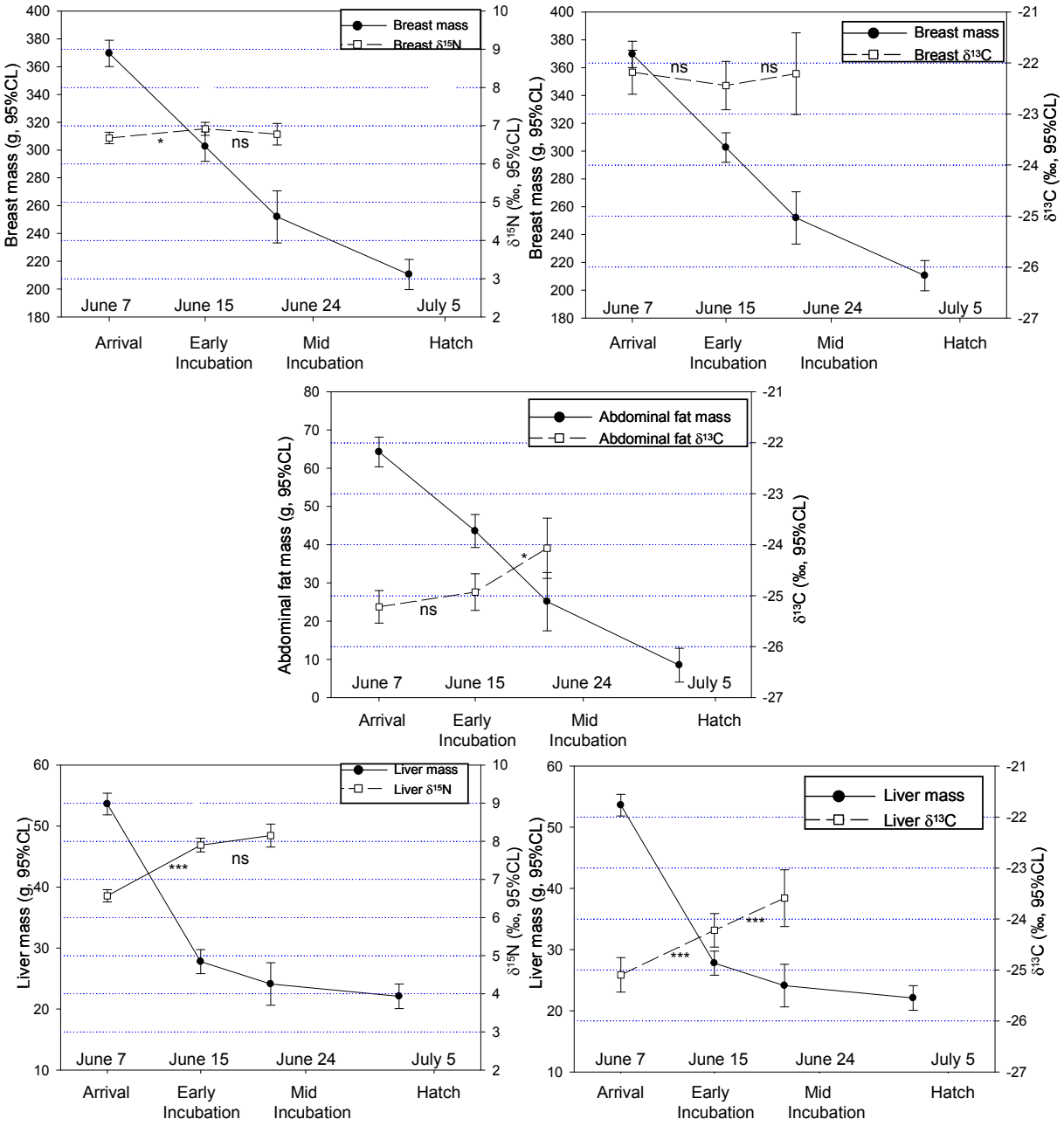


Figure 4.2. Tissue (breast, abdominal fat, and liver) mass and their isotopic values through time for snow geese collected at the Karrak Lake light goose colony, south of Queen Maud Gulf, Nunavut, Canada. Tissue mass values are located on the left y-axis, while stable isotope values are located on the right y-axis. Birds were collected throughout breeding, from arrival, early incubation (< 6 d), mid-incubation (7-10 d), and at hatch (17-23 d). Symbols near dashed lines indicate whether there are differences in isotopic values between successive time periods (* P< 0.05, ** P <0.01, *** P<0.001, ns indicates P>0.05).

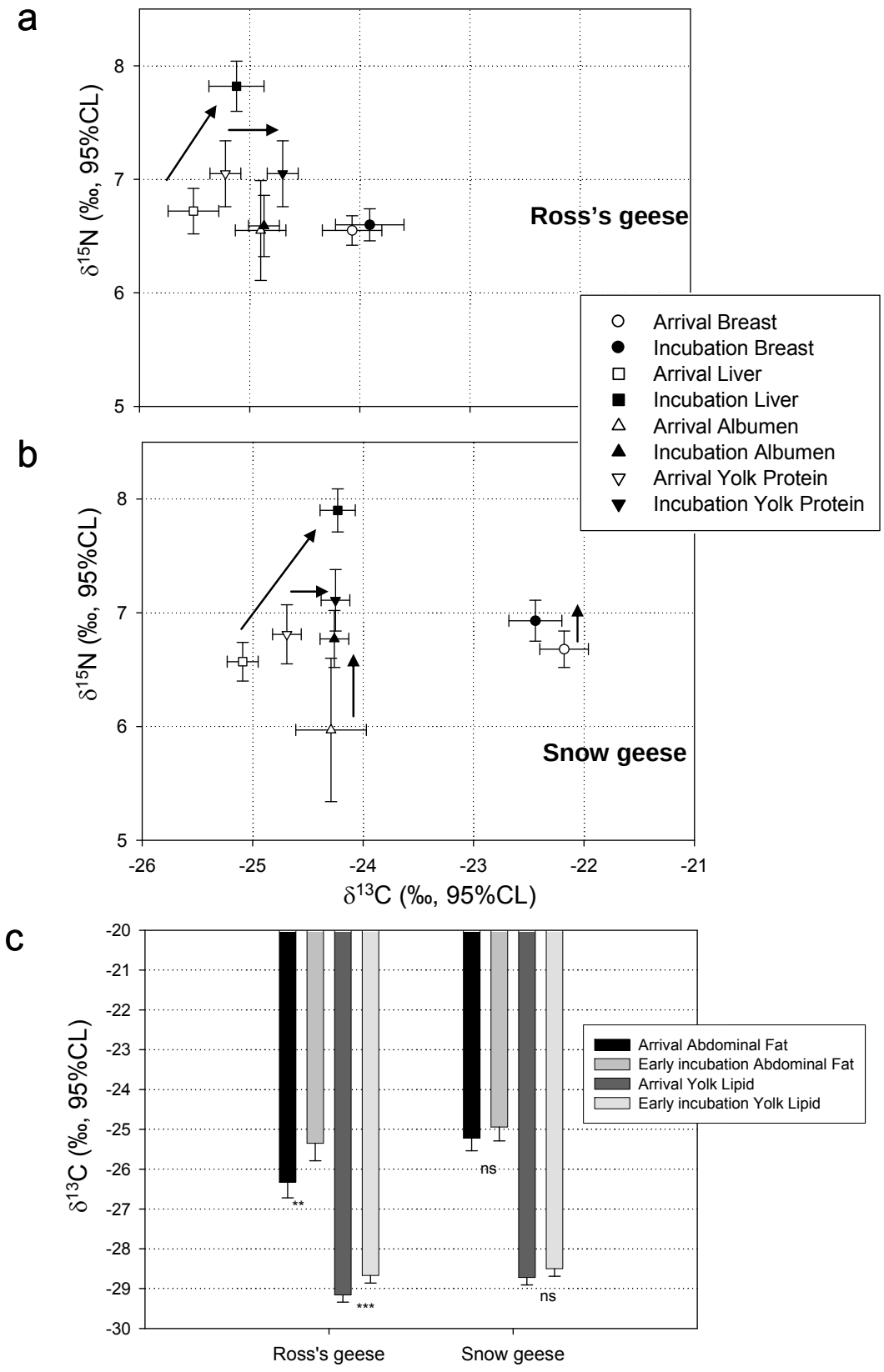

a
b
c
δ15N (‰, 95%CL)
δ13C (‰, 95%CL)
Ross's geese
Snow geese
Arrival Breast
Incubation Breast
Arrival Liver
Incubation Liver
Arrival Albumen
Incubation Albumen
Arrival Yolk Protein
Incubation Yolk Protein
Arrival Abdominal Fat
Early incubation Abdominal Fat
Arrival Yolk Lipid
Early incubation Yolk Lipid
**
***
ns
ns

Figure 4.3. Change in mean isotopic signatures of breast, liver, albumen, and yolk protein for a) Ross's and b) snow geese and c) differences in abdominal fat and yolk lipid in arriving and early incubation at the Karrak Lake light goose colony, south of Queen Maud Gulf, Nunavut, Canada. Black arrows within figures a) and b) indicate significant change among the two groups (horizontal arrows indicate change in $\delta^{13}C$ values, vertical arrows indicate change in $\delta^{15}N$, and diagonal arrows indicate change in $\delta^{15}N$ and $\delta^{13}C$ values. In figure c), symbols below the bars indicate whether there are differences in isotopic values between the two time periods (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, ns indicates $P > 0.05$).

5. LONG-TERM VARIATION IN CLUTCH SIZE AND NEST SUCCESS IN ROSS'S AND LESSER SNOW GEESE

5.1 INTRODUCTION

Life history traits such as timing of reproduction, number and size of offspring, and acquisition and allocation of resources for reproduction and self maintenance can have profound influences on population dynamics (Stearns 1992). A fundamental interest of population ecology is the interplay of ecological factors on components of recruitment, which is also a predominant factor associated with life history variation (Stearns 1992). Life history also covaries with body size among species (Peters 1983). As well, intraspecific variation in body size is the cumulative result of genetic and environmental influences (Boag and van Noordwijk 1987) in turn affecting its adaptiveness when ecological conditions change (Harvey and Purvis 1999). When two closely-related, yet different-sized, species are sympatric breeders, it provides an opportunity to examine the interplay of ecological factors and body size on differences in local population trajectory.

Ross's (*Chen rossii*) and lesser snow geese (*Chen caerulescens caerulescens*, hereafter snow geese) are different-sized arctic-breeding geese that are closely related (99.7% similarity of DNA) (Avise et al. 1992, Hebert et al. 2004) and breed sympatrically within large colonies. The Ross's goose is the smallest of the North American light geese and is considered a smaller form (66% size) of the snow goose (Anderson et al. 1992). Historical population growth rate from 1967 to 1988 of a local population of snow geese was 16.7%, a rate double that of sympatric nesting Ross's geese (Kerbes 1994). However, since then, Ross's geese populations have grown at 11.0% per year, a rate roughly double that shown by snow geese (Alisauskas unpubl. data). Several mechanisms exist for this difference in population growth, although life history theory predicts that populations under nutritional stress, such as can happen in density-dependent fashion, generally respond through declines in recruitment (Eberhardt 2002). Alisauskas (2002) suggested that long-term declines evident in age ratios (immature:adult) of snow geese harvested in the midcontinent of North America were a result of density dependence at the superpopulation level, similar to patterns uncovered at local population scale (Cooch et al. 1991b). Harvest age ratios of Ross's geese are about twice as high as those for snow geese; since relative vulnerability to harvest of young are about equal between species (Chapter 6), this suggests that

Ross's geese tend to have considerably higher recruitment than do snow geese. To understand the role of recruitment in the interspecific divergence in population trajectories, I set out to understand the extent to which components of recruitment during nesting, specifically clutch size and probability of nest success, respond to variation in ecological conditions shared by both species.

Clutch size is a critical determinant of recruitment in birds (Lessells 1986, Johnson et al. 1992). Intrinsic (female condition, size, age) and extrinsic (timing of reproduction, weather) factors are known to influence clutch size (reviewed by Johnson et al. 1992). However, variation in clutch size of colonial geese that breed in the arctic is governed primarily by arrival body condition (Ryder 1970, Ryder 1972, Ankney and MacInnes 1978, MacInnes and Dunn 1988, Hamann and Cooke 1987). Because some species of arctic-breeding geese initiate ovarian development before arrival onto arctic breeding grounds, the need for access to nutrients at nesting sites, often unavailable due to snow cover, is supplanted by nutrient supply to eggs from body reserves stored during migration (Ankney and MacInnes 1978, Ankney 1984, but see Gauthier et al. 2003). Endogenous nutrient reserves in both Ross's and snow geese at Karrak Lake show an interplay with phenology of arrival by birds to the colony as well as the progression of snowmelt (Chapter 3). Such an interplay is known to influence population-level variation in recruitment in snow geese (Alisauskas 2002). Likewise, density-dependent declines in per capita food resources on spring staging areas may be a relatively new proximate factor impinging on the ability to store reserves with concurrent reductions in clutch size and nest success (Cooch et al. 1989, Cooke et al. 1995, Sedinger et al. 1998).

Nest success (the probability that at least one egg hatches in a nest) can be a bottleneck for recruitment (Cowardin and Blohm 1992, Johnson et al. 1992, Hoekman et al. 2002), and can be influenced by numerous ecological factors that influence the likelihood with which nests are depredated, abandoned, or destroyed (Afton and Paulus 1992, Flint and Grand 1996). Predation is the most important proximate cause of nest failure in birds (Martin 1995), although failure by arctic-breeding geese to store sufficient nutrient reserves for high nest attendance and completion of incubation may lead to increased predation (see below). Birds often adopt strategies to reduce predation risk, including (1) placing nests in sites not accessible to predators; (2) dispersing nests over vast areas to reduce likelihood of detection; (3) constructing cryptic nests in cover; and (4) nesting in colonies, where ample food resources may satiate predators or where population

numbers may enable nesting birds to deter predators through aggressive defense (Owen and Black 1990). Despite aggregating in large colonies to reduce predation, nests of arctic geese may still be destroyed by predators depending upon whether nests are placed in upland or lowland habitats (Lecomte et al. 2009) or during years of low small mammal prey numbers (Bêty et al. 2002). However, some predators may be deterred by aggressive defense of nests (Samelius and Alisauskas 2001). In addition, predation may interact with nutritional condition of incubating birds. For example, studies suggest that nest success of arctic geese is predictably higher for nests initiated earlier in the season or in benign weather conditions, given that later nesting birds are likely in poorer condition and inclement weather increases use of somatic reserves (Ankney and MacInnes 1978, Raveling 1989) leading to reductions in nest attendance and increased likelihood of predation.

In this study, I estimated clutch size and nest success of Ross's and snow geese at the Karrak Lake goose colony from 1993 to 2008. My objective was to examine long-term changes and test hypotheses about interspecific differences in relation to timing of reproduction, spring nutrition, local weather conditions, nesting densities (nest success only), and nesting habitat (nest success only). I predicted how each species might respond differently to annual ambient conditions at the colony and how this interplays with the spring storage of nutrient reserves. Large body size of snow geese permits greater storage capacity for endogenous reserves but also predisposes them to absolutely greater nutritional demands than Ross's geese. Additionally, larger body size of snow geese means that they require a longer breeding season and thus depart for northern staging areas and breeding colonies before Ross's geese (Dzubin 1965, Klaassen et al. 2006). Inclement weather may shortstop vanguard snow geese and prevent food acquisition causing geese to rely on limited endogenous reserves for energy metabolism (Barry 1962). Notably, I previously documented that snow geese, in comparison to Ross's geese, have shown absolutely greater reductions in spring arrival nutrition and rely progressively more on somatic reserves for clutch formation once arriving onto the breeding colony (Chapter 3, 4). Thus, through time, I predicted greater declines in clutch size and nest success by snow geese, which would also experience greater decreases in each with (1) poorer body condition, (2) later timing of reproduction, and (3) inclement weather (clutch size only). However, inclement weather during nesting should favor snow geese since larger body size increases fasting endurance and heat retention (Calder 1972). An understanding of ecological factors that influence clutch size

and nest success may lead to improved knowledge of processes responsible for population change of mid-continent snow and Ross's geese.

5.2 METHODS

Data on clutch sizes and nest success were obtained from nest plots placed systematically throughout the nesting colony on a 0.5 km grid system in areas of high density and a 1 km grid system in areas of low density following the Universal Transverse Mercator grid system. Plots were circular and 30 m in radius; a tape measure was extended from the centre of the nest plot and all nests within were numbered and recorded. Clutch size, egg size, nest habitat type, and distance (nearest 0.1m) and angle to the centre of the plot were also recorded. Because birds flush off nests during nest plot visits, I determined goose species from length and width measurements of their eggs (accuracy of classification between 89 and 100%; Alisauskas et al. 1998). Nest initiation dates were estimated by subtracting stage of embryonic development (i.e., obtained by candling eggs) and clutch size from the day the nest was found (Weller 1956). After initial plot visits during incubation, plots were re-visited after hatch and colony exodus to ascertain nest fate. Nests were considered successful when $\geq$ one egg hatched as determined by presence of egg cap, egg membrane, and/or gosling down.

5.2.1 Ecological covariates

Weather. - Severe arctic springs (low temperatures and snow cover) can inhibit access to food, delay migration, and increase energy expenditure, predictably reducing female body condition, which in turn decreases clutch size (Ryder 1970, Ankney and MacInnes 1978, Ely and Raveling 1984). To create a spring severity index, I used weather data from the 3 nearest communities: Cambridge Bay (69˚ 06′ N, 105˚ 08′ W), Baker Lake (64˚ 18′ N, 95˚ 04′ W), and Gjoa Haven (68˚ 38′ N, 95˚ 51′ W). June temperatures were averaged across the stations and May and June snow depths were summed separately across the stations (Alisauskas 2002). Because there was no snow at any of the above mentioned stations at the end of June I used snow depth for early-June (up to June 7). I believe that this permitted valid inference to be drawn about the relationship between clutch size and spring severity at latitudes arriving geese likely experienced on their northward migration as I predicted harsh springs would decrease clutch size geese. I used mean June temperature, total May snow depth, and early-June snow depth in a PCA to

construct a spring severity index. PCA of the correlation matrix resulted in PC1 with loadings of -0.48, 0.60, and 0.63; PC1 accounted for 69% of the summed variance of the three variables. Thus, PC1 was used as a weather index (SEVERITY) and positive PC1 values corresponded to lower mean June temperatures and deeper snow cover in late-May and early-June. Finally, I created a nesting weather index by calculating the mean wind chill (WC) during the nesting period (nest initiation through incubation) per year (Drake 2006). I believed that lower temperatures during nesting would reduce nest success (Harvey 1971).

Timing of reproduction.- Seasonal delays in nesting can deplete stored nutrients before breeding begins or ends which can reduce clutch size or nest success, respectively (Barry 1962, MacInnes and Dunn 1988, Prop and de Vries 1993). I hypothesized decreased reproductive effort (low clutch size or nest success) in years of late spring. Timing of nest initiation is governed by the disappearance of snow and exposure of nesting habitat; usually "late" years result when snow melt is delayed. I used mean nest initiation date calculated for each species separately to create an early-late index (ELI) of timing of nesting. The ELI was calculated as the difference between the annual mean and the long-term average nest initiation dates for 1993-2008.

Arctic geese also experience seasonal declines in clutch size and nest success, which are likely a result of a tradeoff of energy use and reproduction (Ely and Raveling 1984, Rohwer 1992, but see Hamann and Cooke 1989 for review). Subsequently, I used absolute nest initiation (NID) of each nest and also created a relative nest initiation date (RNID) to examine their importance to clutch size and nest success. NID may be more important if each is influenced by the calendar date which females nest each year. For instance, individuals may use photoperiod as a cue to breed and then make timing adjustments based on local conditions (Winkler et al. 2002, Wilson 2007). Conversely, RNID, which is the timing of nesting relative to other females in the same year, may be more important if clutch size or nest success is influenced by spring phenology (Wilson 2007). For nests located during egg-laying, nest initiation was calculated by subtracting the number of eggs in the nest, less one, from the date of discovery. Nest initiation of nests found during incubation were obtained by subtracting stage of embryonic development (Weller 1956) and clutch size (assuming 1 egg = 1.2 d for Ross's geese and 1.4 d for snow geese; Ryder and Alisauskas 1995, Mowbray et al. 2002) from the day the nest was found.

Nutritional condition. - Because of the importance of endogenous reserves to breeding arctic geese (Ryder 1970, Ankney and MacInnes 1978), I created annual indices of fat

(abdominal fat; FAT) and protein (sum of one breast and one bone-free leg; PROTEIN) condition from birds collected during arrival onto the breeding colony for each species separately. Previously, I documented significant decreases in both reserves through time, likely from decreasing per capita forage availability on northern staging areas (Cooch et al. 1989, Abraham and Jefferies 1997, Jefferies et al. 2004). Fat and protein reserves were corrected for structural size, potential clutch size, percent clutch formed at collection period, and collection date (see Chapter 3). Fat and protein indices were calculated as the difference between the annual mean and the long-term average for each nutrient from 1993-2008. Fat and protein condition were used in analyses of clutch size because both may be important to clutch formation (Bon 1997, Croft 1999), though fat is generally the limiting nutrient in temperate breeding waterfowl (Ankney et al. 1991). However, I only considered fat in nest success models because it is likely the most important in the female's ability to complete incubation. Specifically, Alisauskas (2002) demonstrated the importance of fat reserves in the annual recruitment of snow geese at the superpopulation level.

Population size. - Geese nesting in large, dense aggregations should experience higher rates of nest success because the number of losses to predators should decrease through a swamping effect (Raveling 1989, Bêty et al. 2001). By contrast, nest success is predicted to be lower in low density areas since there are fewer adult geese to defend against predators (Armstrong 1998). I included both nesting population size (POP) and nest density (NESTS) in my models. Population size of the breeding colony, in a given year, was calculated based on stratified sampling using sample plots placed throughout the breeding colony on a 0.5 km grid system in areas of high density and a 1 km grid system in areas of low density (Alisauskas et al. 2011a). The total numbers of nests per plot were counted and were indicative of breeding pairs (see Alisauskas and Rockwell 2001). I used the quotient of population size in a given year divided by the smallest population size (377,956 geese) as a measure of relative size in my models; thus relative population size (POP) ranged from 1.0 to 3.13. Finally, I included number of nests per plot (60 m diameter) as a surrogate for nesting density. This was a plot-specific covariate, which I treated as a continuous variable.

Nest habitat. - Because nesting habitat can be an important component of reproductive success (Jackson et al. 1987, Tremblay et al. 1989), I considered habitat characteristics

(HABITAT) of the nest (birch [*Betula spp*.], heath, rock, sand, exposed, moss, mixed; Mclandress 1983) in my nest success analysis.

5.2.2 Statistical analysis: clutch size

I recognized that observed clutch sizes in nests may be different from true clutch size due to egg dumping on staging areas or breeding colony, partial predation, and/or nest parasitism (Cooch et al. 1989, Cooke et al. 1995, Lindberg et al. 1997). Clutch sizes ≥ 7 were considered large and possibly parasitized and were not considered in the analysis (Lank et al. 1989, Ryder and Alisauskas 1995, Mowbray et al. 2000). I considered effects of SPECIES, year (YEAR, linear trend through time), POP, FAT, PROTEIN, spring conservation hunt (HUNT; see below), NID, RNID, ELI, SEVERITY, and *a priori* two-way interactions (i.e., SPECIES*YEAR, SPECIES*POP, SPECIES*FAT, SPECIES*PROTEIN, SPECIES*HUNT, SPECIES*NID, SPECIES*RNID, SPECIES*ELI, SPECIES*SEVERITY). Although there are *a priori* reasons for nonlinear effects in response variables, I did not consider them here. I examined the Pearson product-moment correlation among potential covariates before constructing my candidate set to avoid the possibility of models with severe multicollinearity. Covariates of YEAR, HUNT, FAT, and PROTEIN were highly correlated (r's $\geq |0.65|$). NID was highly correlated with RNID and ELI (r's ≥ 0.63), although RNID and ELI were not correlated ($r = 0.01$) and so were considered together in models. FAT was correlated with ELI ($r = -0.76$). Finally, ELI was correlated with SEVERITY ($r = -0.62$), though I considered them jointly in some models since in exploratory models they did not produce spurious results. Moreover, recent evidence suggests the relationship between ELI and SEVERITY has become decoupled because geese are arriving later to breed due to decreased per capita food availability on staging areas (Chapter 3).

I first considered models with YEAR since such changes in parameters over time may be consistent with links to density dependence. I then considered models with PROTEIN to examine the importance of protein to clutch formation. However, I earlier demonstrated reductions in protein reserves through time so relationships with PROTEIN may imply associations with density dependence as well. I then considered an effect of FAT in competing models to examine its importance to clutch size. Finally, the spring conservation hunt has been documented to decrease body condition and reproductive output in greater snow geese (*Chen caerulescens atlantica*) from disturbance hunting creates during feeding episodes on Canadian

agricultural staging areas (Fèret et al. 2003, Mainguy et al. 2003), so I included HUNT in models to compare differences in clutch size between years with no hunt (1993 to 1998) and a hunt (1999 to 2008). I started with the most saturated model with YEAR, including all interactions {SPECIES, YEAR, RNID, ELI, SEVERITY, SPECIES*YEAR, SPECIES*RNID, SPECIES*ELI, SPECIES*SEVERITY} to examine changes in clutch size through time. Initially, I used generalized linear models (Poisson regression, Proc Genmod, SAS Institute 2008) with the ESTIMATE option for parameter estimation to examine change in clutch size because clutch sizes are count data. However, models assuming Poisson distribution did not fit the data well as they were severely under-dispersed (Goodness of Fit; deviance/df = 0.27); a deviance/df quotient close to 1.0 indicates good model fit (Agresti 1996, Burnham and Anderson 2002). Consequently, I used a normal distribution, which improved model fit (deviance/df = 0.93). Progressively less complex models were then constructed with all covariates. I used an intercept only model as my null model and built 37 candidate models for my analysis of clutch size. I assessed final model strength by measuring % deviance explained; a measure analogous to the coefficient of determination (R^2) in least squares regression (Cameron and Windmeijer 1997).

5.2.3 Statistical analysis: nest success

I used generalized linear models with a binomial response distribution and logit link function (Logistic regression, Proc Genmod, SAS Institute 2008) with the ESTIMATE option for parameter estimation to examine hypothesized differences between species and pertinent factors influencing nest success. I expressed nest success as apparent nest success i.e., [successful nests / (successful nests + unsuccessful nests)]. I included nests that had failed before my arrival onto the nest plot. I assumed this was valid because detection probability of all nests is ~1 (Alisauskas unpubl. data). Fates of neighboring goose nests have been found to be independent of each other in some colonial arctic nesting geese (Bêty et al. 2002), though in my study nest densities are significantly higher (110 to 670 nests per km^2 versus 5000 nests per km^2). Finally, I believed that disturbance to visiting nests during incubation was trivial. Other studies have documented high depredation rates from glaucous gulls (*Larus hyperboreus*) and parasitic jaegers (*Stercorarius parasiticus*) during nest visits (MacInnes 1962, Raveling 1989, Caswell 2009) but at Karrak

Lake arctic foxes (*Alopex lagopus*) are the primary predators. I have never seen arctic fox or avian predators take goose eggs during my activities on nest plots.

In my models, I considered effects of SPECIES, YEAR, POP, FAT, HUNT, NID, RNID, ELI, WC, clutch size (CS; see below), NESTS, HABITAT, and *a priori* two-way interactions (i.e., SPECIES*YEAR, SPECIES*POP, SPECISE*FAT, SPECIES*HUNT, SPECIES*NID, SPECIES*RNID, SPECIES*ELI, SPECIES*WC, SPECIES*CS, SPECIES*NESTS). Although there are *a priori* reasons for nonlinear effects in response variables, I did not consider them here. Before beginning the analysis, I examined the Pearson product-moment correlation among potential covariates to avoid the possibility of models with severe multicollinearity. Covariates of YEAR, POP, HUNT, and FAT were highly correlated (r's $\geq |0.63|$). NID was highly correlated with RNID and ELI (r's ≥ 0.63), although RNID and ELI were not correlated (r = 0.01) and so were considered together in models. Finally, FAT was correlated with ELI (r = -0.76), but was less correlated with NID (r = -0.59) and so FAT and NID were included in models together.

I first considered models with YEAR to specifically test whether nest success showed a unidirectional trend over time since such changes in parameters over time may be consistent with links to density dependence. I then considered an effect of FAT in competing models to examine its importance to clutch size. Next, I considered models with POP since nest success is predicted to increase with greater numbers of nesting geese. Finally, the spring conservation hunt has been documented to reduce reproductive output in greater snow geese (Fèret et al. 2003, Mainguy et al. 2003), so I included HUNT in models to compare differences in nest success between years with and without a hunt. I included CS for each nest as a continuous variable to index female reproductive investment (Bourgeon et al. 2006, Harriman 2006). Studies have shown that nest success is directly related to clutch size such that nests with larger clutch size have higher success (Ackerman et al. 2003, Bourgeon et al. 2006). I started with the most saturated model with POP, including pertinent two-way interactions {SPECIES, POP, FAT, RNID, HABITAT, NESTS, WC, CS, SPECIES*POP, SPECIES*FAT, SPECIES*RNID, SPECIES*NESTS, SPECIES*WC, SPECIES*CS} to examine changes in nest success. My starting model fit the data well (Goodness of fit; deviance/df = 0.96). Progressively less complex models were then constructed for each set. I did not consider all possible combinations of covariates because I wanted to reduce the number possible permutations (e.g., Doherty et al. 2002). I used an

intercept only model as my null model. I considered a total of 29 models for my analysis of nest success. I assessed final model strength by measuring % deviance explained; a measure analogous to the coefficient of determination (R^2) in least squares regression (Cameron and Windmeijer 1997).

5.2.4 Model selection and parameter estimation

I used the information theoretic approach based on Akaike's Information Criterion for model selection (Burnham and Anderson 2002). I used model weight (w_i) to evaluate likelihood of each model; w_i are normalized Akaike weights and indicate the relative support for different models in the candidate model set, and can be interpreted as the evidence that a model is the most plausible, given the data and model set (Burnham and Anderson 2002). I summed w_i of all models (i.e., $\Sigma\, w_i$) with a given covariate and used this as a metric to assess importance (Burnham and Anderson 2002). I considered models $\leq 2\ \Delta$ AIC units to be of similar quality. I generated model-averaged estimates of parameters and unconditional standard errors from a confidence set of models, from which the evidence ratio was ≥ 0.125, if model uncertainty was present (Burnham and Anderson 2002).

Because model-averaged parameters ($\bar{\hat{\beta}}$) from logistic models are not estimates of linear relationships but are log-odds, I exponentiated [$\exp(\bar{\hat{\beta}})$] these parameters to create odds ratios and ease interpretation (Allison 1999). Odds ratios evaluate the effect size of the variables to the outcome (hatch or fail). Associated variances for odds ratios were obtained by exponentiating lower and upper 95% confidence limits of log-odds (Allison 1999). Odds ratios of 1.0 imply no effect on nest success, and thus 95% confidence limits that overlap 1.0 indicate that the covariate does not significantly influence survival. Odds ratios > 1 indicate a positive relationship, while odds ratios < 1 indicate a negative relationship. However, model-averaged parameters still reveal the direction and relative strength of each effect. Thus, I back-transformed slopes and intercepts to make predictions about nest success | $x_1 \ldots x_n$, following

$$\hat{NS}_i = \frac{1}{1+e^{-\left(\hat{\beta}_0+\hat{\beta}_1 x_1+\hat{\beta}_2 x_2+\hat{\beta}_n x_n\right)}}$$

where $\hat{\beta}$ are parameters associated with each explanatory variable.

5.3 RESULTS

5.3.1 Clutch size

I examined 10,739 and 10,270 clutches of Ross's and snow geese, respectively from 1993 to 2008. Overall, mean clutch sizes of snow geese ($\bar{x}_{snow}$ = 3.35, 95% CL: 3.31, 3.38) were 5.0% higher compared to Ross's geese ($\bar{x}_{Ross's}$ = 3.18, 95% CL: 3.14, 3.21). Clutch size varied from 2.79 to 3.64 eggs and 2.87 to 3.69 eggs for Ross's and snow geese, respectively (Fig. 5.1).

The best approximating model describing variation in clutch size included additive effects of SPECIES, PROTEIN, RNID, ELI, SEVERITY; with interaction effects of SPECIES*PROTEIN and SPECIES*SEVERITY (Model {1}, w_i = 0.52, Table 5.1). A second competing model (w_i = 0.21, ΔAIC = 1.82) was similar to the top-ranked model but included an interactive effect of SPECIES*RNID (Table 5.1, Model {2}). Finally, a third ranking model (w_i = 0.18, ΔAIC = 2.10) was analogous to the second ranking model but had an interactive effect of SPECIES*ELI instead of SPECIES*SEVERITY (Table 5.1, Model {3}). Top models explained only 7.7% of deviance in clutch size, suggesting variables not included in competing models may have had a larger impact on clutch size than those modeled. All other models had ΔAIC $\geq$ 4.22 and so had little support relative to the three best models. Moreover, models that included covariates such as YEAR, FAT, and HUNT were of even lower quality (ΔAICs $\geq$ 11.61).

Overall, clutch sizes displayed robust relationships with protein reserves. Clutch size increased with larger protein reserves in snow geese (coded as '0' in design matrix) ($\overline{\hat{\beta}}_{protein(snow)}$ = 0.0022, 95% CL: 0.0014, 0.0031; Σw_i = 1.0). However, a SPECIES*PROTEIN interaction ($\overline{\hat{\beta}}_{species*protein(ross)}$ = 0.0029, 95% CL: 0.0009, 0.0049; Σw_i = 1.0) suggested Ross's geese (coded as '1' in design matrix) experienced greater increases in clutch size with larger protein reserves than did snow geese ($\overline{\hat{\beta}}_{protein(ross)}$ 0.0051, 95% CL: 0.003, 0.007) (Fig. 5.2). Clutch size also decreased in years of late reproduction ($\overline{\hat{\beta}}_{ELI(snow)}$ = -0.050, 95% CL: -0.055, -0.045; Σw_i = 1.0); there was some support for a SPECIES*ELI interaction ($\overline{\hat{\beta}}_{species*ELI(ross)}$ = 0.004, 95% CL: 0.02, 0.06; Σw_i = 0.24) that suggested Ross's geese experienced smaller decreases in clutch size in later years ($\overline{\hat{\beta}}_{ELI(ross)}$ = -0.046, 95% CL: -0.05, -0.04). I found strong support for the inclusion of RNID versus NID in my models; there were seasonal reductions in clutch size ($\overline{\hat{\beta}}_{RNID(snow)}$ = -0.035, 95%

CL: -0.040, -0.030; $\Sigma w_i = 1.0$). Still, there was some indication (SPECIES*RNID interaction, $\Sigma w_i = 0.42$) that female Ross's geese experienced smaller decreases in clutch size with advancing relative nest initiation dates ($\overline{\hat{\beta}}_{species*RNID(ross)} = 0.0054$, 95% CL: -0.0018, 0.013) ($\overline{\hat{\beta}}_{RNID(ross)} = -0.030$, 95% CL: -0.04, -0.02) than did female snow geese, though results were equivocal. Finally, there was evidence of different trends in clutch size with severe arctic springs among species (SPECIES*SEVERITY; $\Sigma w_i = 0.75$, $\overline{\hat{\beta}}_{species*severity} = 0.037$, 95% CL: 0.018, 0.056). Specifically, Ross's geese did not display decreases in clutch size with severe springs ($\overline{\hat{\beta}}_{severity(ross)} = 0.022$, 95% CL: 0.005, 0.039) as did snow geese ($\overline{\hat{\beta}}_{severity(snow)} = -0.015$, 95% CL: -0.03, 0.00).

There was no support for models with YEAR, FAT, or HUNT ($\Sigma w_i = 0.00$) (Table 5.1). However, these covariates describing variation in clutch size were precisely estimated allowing interpretation of their effects. A top model with YEAR {Species, YEAR, RNID, ELI, SEVERITY, SPECIES*YEAR, SPECIES*SEVERITY} (ΔAIC = 30.92) suggested differences in decline of clutch size through time between species (SPECIES*YEAR; $\hat{\beta}_{species*year(ross)} = 0.0055$, 95% CL: 0.00, 0.01). In particular, snow geese experienced larger decreases in clutch size through time ($\hat{\beta}_{year(snow)} = -0.010$, 95% CL: -0.015, -0.006) compared to Ross's geese ($\hat{\beta}_{year(ross)} = -0.005$, 95% CL: -0.01, 0.00). The best model with FAT (Table 5.1, Model {6}) suggested that clutch size of both species increased with larger fat reserves ($\hat{\beta}_{fat} = 0.005$, 95% CL: 0.004, 0.006). Finally, the top model with spring conservation hunt {Species, HUNT, RNID, ELI, SEVERITY, SPECIES*HUNT, SPECIES*SEVERITY} (ΔAIC = 24.91) suggested that snow geese collected during the period preceding efforts to reduce population size (until 1998) had larger clutch sizes than during efforts of population reduction (after 1998) ($\hat{\beta}_{hunt(snow)} = 0.13$, 95% CL: 0.08, 0.17). Nonetheless, a significant SPECIES*HUNT interaction ($\hat{\beta}_{species*hunt(ross)} = -0.10$, 95% CL: -0.16, -0.04) suggested little influence of the conservation hunt on Ross's goose clutch sizes ($\hat{\beta}_{hunt(ross)} = 0.03$, 95% CL: -0.03, 0.07). Least-square means showed no change in Ross's geese (No hunt = 3.22, 95% CL: 3.18, 3.26; hunt = 3.20, 95% CL: 3.18, 3.22; P = 0.31), while snow geese displayed significant decreases in clutch size in response to the spring hunt (No hunt = 3.42, 95% CL: 3.38, 3.45; hunt = 3.29, 95% CL: 3.27, 3.31; P < 0.0001). HUNT was

related to, and confounded with, YEAR, FAT, and PROTEIN; it was difficult to conclusively separate their effects on clutch size. Although, parameter estimates relating clutch size to the conservation hunt were largely different from zero, the apparent effect of HUNT was likely spurious. Model quality was superior if clutch size were structured against PROTEIN rather than HUNT.

5.3.2 Nest success

I examined 10,269 and 9,590 nests of Ross's and snow geese, respectively from 1993 to 2008. Overall, mean apparent nest success was ~4.5% higher for Ross's geese ($\bar{x}_{Ross's}$ = 81.28%, 95% CL: 79.18, 83.20%) than snow geese ($\bar{x}_{snow}$ = 76.83%, 95% CL: 74.34, 79.11%). Nest success varied from 69 to 94% and 60 to 90% for Ross's and snow geese, respectively (Fig. 5.3).

My most plausible model explaining variation in nest success included additive effects of SPECIES, POP, RNID, ELI, HAB, NESTS, WC, and CS; with interaction effects of SPECIES*WC, SPECIES*ELI, SPECIES*RNID, and SPECIES*CS (w_i = 0.36, Table 5.2, Model {1}). Other competing models were very similar in structure to the best model and included model {2} (w_i = 0.26, ΔAIC = 0.73) which did not contain an interactive effect of SPECIES*WC, model {3} (w_i = 0.11, ΔAIC = 2.36) which had an effect of YEAR instead of POP, and model {4} (w_i = 0.10, ΔAIC = 2.52) with an interactive effect of SPECIES*NESTS (Table 5.2). All other models had Akaike weights, $\leq w_i$ = 0.08, and ΔAIC $\geq$ 3.14) and so had little support relative to the top models. By contrast, competing models which included FAT (ΔAIC $\geq$ 5.48) and HUNT (ΔAIC $\geq$ 25.32) were of even lesser quality. Overall, top models explained only 6.7% of the deviance in nest success, suggesting that variables not included in competing models may have had a larger impact on nest success than those modeled.

There was strong support for a SPECIES*CS interaction ($\bar{\hat{\beta}}_{species*CS(ross)}$ = 0.23, 95% CL: 0.15, 0.31; Σw_i = 1.00) which suggested that Ross's geese (coded as '1' in design matrix; $\bar{\hat{\beta}}_{CS(ross)}$ = 0.66, 95% CL: 0.60, 0.72) displayed higher rates of nest success with increasing clutch size compared to snow geese (coded as '0' in design matrix; $\bar{\hat{\beta}}_{CS(snow)}$ = 0.43, 95% CL: 0.38, 0.48). Overall, the odds of nest success were higher for Ross's geese with increasing clutch sizes than for snow geese (Table 5.3). The ratio of these two odds ratios (Ross's geese over snow

geese) is the odds ratio for the SPECIES*CS interaction, which suggested the odds of nest success was 1.26 times greater for Ross's geese with increasing clutch size compared to snow geese (Table 5.3). Nest success also increased with warmer relative nesting temperatures, although there were differences in nest success between species in relation to changing ambient conditions (SPECIES*WC; $\Sigma w_i = 1.00$, $\overline{\hat{\beta}}_{species*WC(ross)} = 0.05$, 95% CL: 0.00, 0.10). Specifically, Ross's geese ($\overline{\hat{\beta}}_{WC(ross)} = 0.15$, 95% CL: 0.09, 0.17) displayed higher rates of nest success with increasing relative temperatures compared to snow geese ($\overline{\hat{\beta}}_{WC(snow)} = 0.10$, 95% CL: 0.06, 0.14) (Table 5.3, Fig. 5.4). Additionally, I found substantial evidence of disparate trends in nest success with delays in breeding (SPECIES*ELI; $\Sigma w_i = 1.00$, $\overline{\hat{\beta}}_{species*ELI(ross)} = 0.06$, 95% CL: 0.04, 0.09) such that snow geese experienced lower rates of nest success with increasing lateness ($\overline{\hat{\beta}}_{ELI(snow)} = -0.05$, 95% CL: -0.06, -0.03), while Ross's geese did not ($\overline{\hat{\beta}}_{ELI(ross)} = 0.01$, 95% CL: 0.00, 0.03) (Table 5.3, Fig. 5.4). There was also evidence of seasonal differences between species in nest success (SPECIES*RNID; $\Sigma w_i = 1.00$, $\overline{\hat{\beta}}_{species*RNID(ross)} = -0.04$, 95% CL: -0.06, -0.02). Snow geese that initiated nests later relative to other females displayed increases in nest success ($\overline{\hat{\beta}}_{RNID(snow)} = 0.02$, 95% CL: 0.00, 0.03), while Ross's geese that initiated nests earlier relative to other females had higher nest success ($\overline{\hat{\beta}}_{RNID(ross)} = -0.02$, 95% CL: -0.03, -0.01) (Table 5.3).

My results further suggest that nest success increased with higher nesting densities within a 60 m diameter plot the nest was located in ($\overline{\hat{\beta}}_{nests(snow)} = 0.004$, 95% CL: 0.00, 0.01; $\Sigma w_i = 1.00$), although there was slight support for a SPECIES*NESTS interaction ($\hat{\beta}_{species*nests(ross)} = 0.004$, 95% CL: 0.00, 0.01; $\Sigma w_i = 0.17$) implying that Ross's geese displayed greater increases in nest success with increasing nest densities than snow geese ($\hat{\beta}_{nests(ross)} = 0.004$, 95% CL: 0.00, 0.01). However, in accordance with limited support for the interaction, the odds ratio of the SPECIES*NESTS interaction suggested that there was no difference (Table 5.3). Contrary to prediction, I found evidence that nest success decreased with increasing population size of the breeding colony ($\overline{\hat{\beta}}_{population} = -0.21$, 95% CL: -0.28, -0.15; $\Sigma w_i = 0.74$). The corresponding odds

ratio suggested a large negative effect of population size on nest success (Table 5.3). There was substantial support for the effect of nesting habitat (HAB; $\Sigma w_i = 1.00$) on nest success. Predicted mean estimates from the top model suggest that nest success was lowest on exposed substrates ($\bar{x}_{exposed} = 71.47\%$, 95% CL: 66.40, 76.06%), rock ($\bar{x}_{rock} = 72.47\%$, 95% CL: 69.37, 75.37%), and birch ($\bar{x}_{birch} = 74.95\%$, 95% CL: 72.32, 77.41%), whereas nest success increased on mixed habitats ($\bar{x}_{mixed} = 79.58\%$, 95% CL: 77.51, 81.50%), heath ($\bar{x}_{heath} = 79.57\%$, 95% CL: 77.33, 81.64%), moss ($\bar{x}_{moss} = 82.46\%$, 95% CL: 80.45, 84.30%), and sand ($\bar{x}_{sand} = 86.27\%$, 95% CL: 74.41, 93.28%). Moreover, odds ratios suggested that nest success of nests within habitats of moss (1.34, 95% CL: 1.19, 1.52), mixed (1.28, 95% CL: 1.14, 1.44), and heath (1.30, 95% CL: 1.14, 1.48) was greater than nest success of nests within birch habitat, while nests in exposed habitats had lower nest success (0.68, 95% CL: 0.52, 0.88) compared to nests in birch habitat. The 95% CL of sand (1.96, 95% CL: 0.86, 4.49) and rock (0.94, 95% CL: 0.80, 1.10) included 1.0 suggesting no differences in nest success of nests compared to nests in birch habitat.

There was limited evidence that nest success of both species decreased through time ($\bar{\hat{\beta}}_{year} = -0.03$, 95% CL: -0.04, -0.02; $\Sigma w_i = 0.22$). Moreover, there was no support for models with FAT ($\Sigma w_i = 0.03$) or HUNT ($\Sigma w_i = 0.00$). Nevertheless, these slopes of nest success relative to these covariates were accurately estimated. The top model with FAT {Species, FAT, RNID, HABITAT, NESTS, WC, CS, SPECIES*FAT, SPECIES*RNID, SPECIES*CS} (ΔAIC = 5.48) suggested differential responses in nest success with fat reserves (SPECIES*FAT; $\bar{\hat{\beta}}_{species*fat(ross)} = -0.021$, 95% CL: -0.03, -0.01). Specifically, snow geese realized higher rates of nest success with larger fat reserves ($\bar{\hat{\beta}}_{fat(snow)} = 0.015$, 95% CL: 0.01, 0.02), while Ross's geese displayed slight decreases in nest success with higher fat reserves ($\bar{\hat{\beta}}_{fat(ross)} = -0.008$, 95% CL: -0.01, 0.00). The best model with spring conservation hunt {Species, Hunt, RNID, ELI, HABITAT, NESTS, WC, CS, SPECIES*ELI, SPECIES*RNID, SPECIES*CS} (ΔAIC = 25.32) suggested that nest success of geese was higher when there was no hunt than nest success during the period with the conservation hunt ($\hat{\beta}_{hunt} = 0.13$, 95% CL: 0.08, 0.18). I was unable to conclusively determine whether declines observed in nest success at Karrak Lake following initiation of the conservation hunt in spring of 1999 were due, in fact, to the hunt, or to simultaneous rapid population growth.

Variation in nest success was explained as well as or better by models with POP and FAT, than with the presence of a conservation hunt.

5.4 DISCUSSION

5.4.1 Clutch size

Clutch size in these arctic geese was directly related to the protein condition of arriving female geese. Ankney and MacInnes (1978) documented snow geese relied heavily on protein reserves during egg-laying; more than 29% of the loss in somatic tissue during egg-laying was due to diminished protein stores. Moreover, I found that clutch size in Ross's geese was more sensitive to changes in protein condition than were clutch sizes in snow geese. This stronger relationship may have been related to the small body size of Ross's geese. Ankney (1984) demonstrated that smaller waterfowl species allocated proportionately more nutrients into their respective clutches than did larger species (Chapter 4). Secondly, smaller species have absolutely smaller protein reserves than do larger species (Ankney 1984, Chapter 3). Consequently, when Ross's geese experience reductions in protein reserves clutch size will show more rapid decreases than would clutch size in larger-bodied snow geese. Ultimately, Ross's geese cannot over commit protein reserves to clutch formation since severe reductions in protein will decrease reproductive success and may cause death by starvation (Ankney and MacInnes 1978, Le Maho et al.1981, Cherel et al. 1988).

I previously demonstrated that protein reserves within these arctic geese have displayed significant decreases through time likely from reduced carrying capacity on northern staging areas (Chapter 3). The relationship between reductions in protein condition and concomitant decreases in clutch size are thus, related to density dependence upon staging areas. Cooch et al. (1989) documented a long term decrease in clutch size of 0.72 eggs over 16 years in snow geese and attributed it to decreased food resources on penultimate staging areas. In this 16 year study, Ross's and snow geese were predicted to lose 0.18 and 0.15 eggs, respectively with decreasing protein reserves. Differences in clutch size reductions may be due to differences in spring nutrient acquisition and breeding strategies between the two populations. At the sub-arctic La Pérouse Bay goose colony in Manitoba, geese arrive and forage on the colony eleven days before initiating nests (Mowbray et al. 2000). Thus, because these geese likely rely on breeding colony forage for clutch formation (Ganter and Cooke 1996, Gauthier et al. 2003) and there have been

large reductions in vegetation in the colony, larger decreases in clutch size are apparent. At the arctic Karrak Lake colony, geese initiate rapid follicle development before arrival onto the colony, begin nesting within three days of arrival, and likely utilize proportionately more endogenous reserves for clutch formation (Chapter 4). Thus, geese at Karrak Lake experienced smaller decreases in clutch size because they used endogenous reserves, which provided a more consistent nutrient source for egg synthesis.

In these geese, arrival condition onto breeding areas was the most important determinant of clutch size. I suggest arrival condition in this population is currently decreasing due to reductions in carrying capacity (Chapter 3). Nutritional condition of arriving individuals may also decrease with severe arctic weather and/or timing of reproduction, though geese breeding at Karrak Lake are now breeding later due to decreased per capita food availability, which in turn stalls geese on migratory staging areas (Chapter 3). Both species displayed reductions in clutch sizes with delayed breeding because geese have fewer reserves to partition into developing follicles or geese may display atresia of some developing follicles, which would allow use of nutrients already allocated to egg production (Raveling 1978, Hamann and Cooke 1989). Though not as large as a reduction in clutch size with delayed breeding, snow geese displayed reductions in clutch size with severe arctic springs. Inclement weather can diminish clutch size by denying access to food plants or causing increased energy expenditure thereby reducing endogenous reserves (Ryder 1970, Ankney and MacInnes 1978, Ely and Raveling 1984). Snow geese depart for northern staging areas sooner and have a more protracted spring migration relative to Ross's geese (Dzubin 1965, Ryder and Alisauskas 1995). Thus, inclement weather conditions may shortstop vanguard snow geese and reduce food acquisition causing geese to rely on important, limited endogenous reserves for energy metabolism (Barry 1962). Additionally, snow geese, in comparison to Ross's geese, partition more staging area foods into developing follicles (Chapter 3). Thus, in years of severe arctic weather snow geese experienced greater decreases in clutch sizes than did Ross's geese.

Clutch sizes in both species decreased with progressively later nest initiation dates. In general, this decline was likely a result of a tradeoff in use of endogenous reserves for energy metabolism and reproduction created by later nest initiations (Ely and Raveling 1984, Rohwer 1992, but see Hamann and Cooke 1989 for review). Overall, my results suggest support for relative versus absolute effects of nest initiation date in the formation of clutch size because

northward migration and subsequent ova development of arctic geese is constrained by spring phenology (i.e., local conditions on staging areas) as they migrate following the 0 degree isotherm (Ryder 1970, Raveling 1978). Environmental conditions on staging areas dictate clutch size since they initiate rapid follicle growth before arrival onto nesting areas developing two scenarios: (1) geese forego breeding altogether or (2) geese decrease clutch size to save capital for incubation or energy metabolism (Ankney and MacInnes 1978, MacInnes and Dunn 1988, Alisauskas and Ankney 1990). These effects can be highly variable because some studies have found clutch sizes to increase or remain unchanged with late snow melt (Bruggink et al. 1994, Lindberg et al. 1997).

5.4.2 Nest success

Arctic nesting geese generally nest dispersed across a heterogeneous landscape, in colonies of various sizes or in association with aggressive species to overcome the effects of predation (Tremblay 1987, Baldwin 2006) because predation is the primary cause of nest failure in birds (Martin 1995). I predicted that nest success at the Karrak Lake colony would increase with larger population sizes because the number of losses to predators should decrease through a swamping effect (Raveling 1989, Bêty et al. 2001). Specifically, predation at Karrak Lake should be minimal because nest densities reach 5000 per km^2 (> 1 million geese, Alisauskas et al. 2011a) (Raveling 1989, Samelius and Alisauskas 2006). However, my results suggest that Ross's and snow geese displayed reductions in nest success with increasing population size. I think that intense foraging and nest building activities of geese have denuded nesting habitat such that vegetation available to construct nests may now be limiting in areas regularly used by nesting geese (McCracken et al. 1997, Didiuk et al. 2001, Alisauskas et al. 2006a). Because geese use vegetation to construct nests and proper construction is needed to ensure an adequate thermal environment for embryonic development, any reduction in nesting material may compromise embryo survival and ultimately nest success (McCracken et al. 1997). However, my results suggest that nest success increased with increasing nesting density within the colony. Nesting in dense aggregations would likely deter nest predation through predator swamping or collective defence of nests (Wittenberger and Hunt 1985). Overall, increasing density is thought to decrease nest survival in some species (Stokes and Boersma 2000), though results remain ambiguous in geese (Raveling 1989). Decreases in nest success often result from increased

conspecific interactions, parasite loads, and disease (Stokes and Boersma 2000). For instance, Harriman (2006) documented reductions in nest success of Ross's and snow goose nests with increased numbers of nest ectoparasites at the Karrak Lake colony. Additionally, Ewaschuk & Boag (1972) found increased harassment of incubating female Canada geese (*Branta canadensis*) at high nest densities and decreased nest success in subordinate females. At Karrak Lake, nesting density could be confounded with location since nests on the periphery are generally sparse. However, Armstrong (1998) found that sympatric nesting black brant (*Branta bernicula nigricans*) and snow geese experienced no benefit to nesting in central locations of the colony.

Nesting habitat can also be an important determinant of nest success (Tremblay et al. 1997, Lecomte et al. 2008). My results suggest differential nest success among habitat types. Notably, survival was lowest on exposed habitats. This habitat type likely has inadequate availability of nest building materials; such decreases in building materials can increase nest exposure and inhibit embryo development (McCracken et al. 1997). Though nesting in shrubs generally provides increased nesting success through decreases in predator detection (Jackson et al. 1988), my predicted estimate of nest success in birch tree habitat was lower than moss, mixed, and heath habitats. Notably, some birch habitats at Karrak Lake have extremely high flea (*Ceratophyllus vagabundus vagabundus*) abundance, which have been shown to reduce nest success up to 13% (Harriman et al. 2008).

Alisauskas (2002) documented the importance of fat storage during spring migration to subsequent snow goose recruitment at the superpopulation level and suggested that the mechanism causing diminished recruitment may be reduced fat reserves which render females unable to complete incubation. I predicted, apparently incorrectly, that fat reserves would be an important factor influencing nest success. Still, I did find that nest success decreased in years of delayed breeding thereby suggesting fat reserves may be important because fat reserves predictably decrease with delays in breeding (Chapter 3). Snow goose nest success was twice as sensitive to delays in breeding compared to Ross's geese. I suspect that differential responses to delays in breeding may result from their respective life history strategies. Foremost, snow geese relied on fat reserves for incubation metabolism (Ankney and MacInnes 1978, Chapter 4). Earlier arrival and nesting by snow geese forces greater use of snow-free rocky habitat, heath tundra, and exposed substrates in upland areas of the colony (Alisauskas et al. 2006a). Thus,

nesting in areas with very little nest building vegetation requires high incubation constancy to maintain proper embryo development and survival (McCracken et al. 1997), which in turn requires fat reserves. Delays in breeding, and hence decreases in fat reserves, likely force female snow geese to initiate foraging breaks, which ultimately may reduce embryo development, render females unable to protect nests from predators, or cause nest abandonment (Ankney and MacInnes 1978, Thompson and Raveling 1987, McCracken et al. 1997). By contrast, smaller Ross's geese have absolutely less nutrient reserves and a higher metabolic rate per gram of body weight forcing females to feed more during incubation and thus have lower incubation constancy (Ankney 1984, Schmidt-Nielson 1984, Afton and Paulus 1992, Gloutney et al. 2001, but see Jónsson et al. 2007). Yet, later arrival of Ross's geese permits occupancy of lowland, better-vegetated areas that become available as snow continues to melt and which were previously unavailable to many snow geese; moreover, Ross's geese construct proportionally larger nests with greater insulative ability compared to snow geese (McCracken et al. 1997). Larger nests of Ross's geese likely provide a more suitable thermal environment for the developing embryos compared to snow goose nests thus permitting lower incubation constancy (McCracken et al. 1997). Incubation breaks allow Ross's geese to satisfy some nutritional demands of incubation through local foraging because their smaller size means they have lower energy requirements than larger snow geese (Thompson and Raveling 1987). Further, large nests of Ross's geese reduce energy expenditure since less energy is required to rewarm eggs after incubation breaks (McLandress 1983, McCracken et al. 1997). Thus, delays in breeding and associated decreases in fat reserves are likely not as detrimental to hatching success in Ross's geese. Finally, though differences in arrival times and breeding strategies dictate differential responses to delays in breeding, body size differences create differences in responses to ambient weather conditions during incubation. Snow geese experienced smaller decreases in nest success with decreasing temperatures during incubation compared to smaller-bodied Ross's geese. Larger-bodied birds are more likely to withstand lower temperatures and fast for longer periods of time because of lower body surface area to volume ratios and greater heat retention (Fretwell 1972, Calder 1974, Peters 1983). However, Ross's geese still had higher nest success in colder weather.

I found support for relative nest initiation date versus absolute nest initiation date on nest success suggesting the importance of spring phenology to nesting each year. Spring phenology dictates arrival and timing of reproduction in arctic-breeding light geese, though recently this

relationship has become decoupled due to density dependence on the ability to acquire proper nutrition from northern staging areas (Chapter 3). In general, nest initiation date is negatively related to nest survival (Cooke et al. 1984, Sedinger and Flint 1991). Natural selection should favor the earliest nesting possible, although at the cost of acute responses to current environmental conditions on breeding areas (Cooke et al. 1984). My results suggest differential relationships with seasonal delays in breeding and nest success for each species; snow geese increased nest success and Ross's geese decreased nest success with progressively later nest initiation dates. Because larger-bodied snow geese breed earlier than Ross's geese in highly seasonal habitats, there may be a cost of arriving too early to breed. In my analyses, I only considered linear relationships between nest success and nest initiation. However, Béty et al. (2004) considered the costs of arriving too early and found decreased reproductive success compared to arrival times that were closer to normal. Vanguard snow geese, which initiate nests before most other geese arrive onto the colony, may experience decreased nest success from (1) inclement weather, (2) reliance on limited endogenous reserves which are needed to complete incubation, and/or (3) increased egg loss or nest predation (Harvey 1971, Cooke et al. 1995, Lepage et al. 2000). In particular, nests initiated early may not benefit from colony synchrony because they are more vulnerable to failure due to lack of other active nests (Baldwin 2006).

I also found that nests with larger clutch sizes had higher nest success, which likely results from increased female reproductive investment (Ackerman et al. 2003). However, Ross's geese experienced larger increases in nest success with larger clutch sizes compared to snow geese. Smaller geese should invest more into their clutches because their egg size is larger relative to their body size (Ankney 1984, Dunn and MacInnes 1987, Thompson and Raveling 1987). Increased investment may render Ross's geese more protective of their nests. In particular, Ross's may be more adept at stopping avian predators because their smaller size renders them more maneuverable in flight (Thompson and Raveling 1987), though one would expect Ross's geese to be more vulnerable to arctic fox predation (Anthony et al. 1991, Stickney 1991). McLandress (1983) documented that Ross's geese nesting on islands had the largest clutch sizes in high density plots. Perhaps patterns observed in Ross's goose nest success with larger clutch sizes resulted from high quality females nesting in dense aggregations where conspecifics act as a collective defense against predation? Nevertheless, smaller clutches of both species experienced similarly low nest success given that these females may have been young,

inexperienced, or just in poor condition (Ryder 1970, McLandress 1983). Ultimately, I hypothesize that females with larger clutches realized higher nest success because they nest in better habitats, possibly in higher density areas, are more attentive to their nests, and more successful at deterring mammalian and avian predation attempts (Samelius and Alisauskas 2001, 2006).

Overall, my results demonstrated the importance of spring nutrition on clutch size and nest success in these arctic geese. Decreases in clutch size were primarily related to diminished protein condition of arriving females, while nest success was negatively related to population size and delays in breeding. Clutch sizes of Ross's geese were more sensitive to changes in protein than were snow geese. However, both were predicted to reduce clutch size by only 0.15 and 0.18 eggs over the course of study. Both species of geese showed large declines in nest success through time with increasing population size; nest success was predicted to decrease by 11% for both species. Snow geese had lower probabilities of nest success compared to Ross's geese and the disparity increased with delays in breeding (i.e., from 5% to 13%). Because nest success can be an important variable explaining population dynamics in some waterfowl species (mallard ducks, *Anas platyrynchos*; Hoekman et al. 2002), I think that diminished spring nutrition and delays in breeding from decreased per capita food availability on staging areas may diminish nest success and be a bottleneck to snow goose population dynamics. Alisauskas (2002) suggested that "fat reserves probably have a larger influence on fecundity and recruitment than any relatively small-scale adjustments in clutch size in response to variation in protein or mineral reserves among nesting snow geese". Nonetheless, I suspect that diminished spring nutrition may have affected breeding probability of snow geese because I did not find large disparate trends in nest success between species. The proportion of birds (in a population) that attempt to breed is an important variable in population dynamics and could be a larger bottleneck on local population growth than nest success. For instance, from 2006 to 2008 the number of snow geese breeding at the Karrak Lake colony decreased from 597,421 to 311,676 birds, while numbers of Ross's geese increased from 547,421 to 670, 904 birds (Alisauskas unpubl. data). Reed et al. (2004) provided substantial evidence that nesting densities of greater snow geese (*Chen caerulescens atlantica*) reflected annual variation in breeding probability. In summary, I suggest that body size differences between species dictated their differential migration chronology and patterns of energy use (breeding strategies used for clutch formation and incubation), which I

believe created variation in how their reproductive effort (proportion of adults attempting to breed, clutch size, and nest success) responded to decreases in per capita food availability upon spring staging areas.

Table 5.1. Top models explaining clutch size variation in nests of Ross's (n = 10,739) and snow (n = 10,270) geese at the Karrak Lake light goose colony, south of Queen Maud Gulf, Nunavut, Canada, from 1993 to 2008. Only the seven top models of thirty-seven are shown here, ranked by ascending ΔAIC. The percent deviance explained of the top model was 7.7% [a].

Number/Model[b]	AIC[c]	ΔAIC[d]	w_i^e	K[f]	-2 Log L[g]
1 {Species, Pro, RNID, ELI, Severity, Species*Pro, Species*Severity}	55563.61	0.00	0.52	12	-27769.80
2 {Species, Pro, RNID, ELI, Severity, Species*Pro, Species*Severity, Species*RNID}	55565.43	1.82	0.21	14	-27768.71
3 {Species, Pro, RNID, ELI, Species*Pro, Species*RNID, Species*ELI}	55565.71	2.10	0.18	11	-27771.85
4 {Species, Pro, RNID, ELI, Species*Pro, Species*ELI}	55567.83	4.22	0.06	11	-27772.91
5 {Species, Pro, RNID, ELI, Severity, Species*Pro, Species*Severity, Species*RNID, Species*ELI}	55569.28	5.68	0.03	16	-27768.64
6 {Species, Fat, NID, Severity, Species*Severity}	55575.21	11.61	0.00	9	-27778.61
7 {Species, Fat, NID, Severity, Species*Fat, Species*Severity}	55578.88	15.27	0.00	11	-27778.44

[a] A measure analogous to the coefficient of determination (R^2) in least squares regression (Cameron and Windmeijer 1997).

[b] Model factors included Species, NID (absolute time of nest initiation, calendar date), RNID (timing of nesting relative to other females of the same species in the same year), ELI (early-lateness index, difference between annual mean nest initiation and long-term average from 1993 to 2008), Severity (index of spring weather; mean June temperature and total snow depth at end of May and early June), Fat (annual index of abdominal fat from arriving birds collected at the breeding colony, done for each species separately), Pro (annual index of protein [one breast + one bone-free leg] from arriving birds collected at the breeding colony, done for each species separately), and * (asterisk, denotes interaction between variables; otherwise effects are additive).

[c] Akaike's Information Criterion.

[d] Difference in AIC values between the model with the lowest AIC value.

[e] Estimates of the likelihood of the model, given the data; normalized to sum to one (Burnham and Anderson 2002).

[f] Number of estimable parameters.

[g] – 2log-likelihood of the current model.

Table 5.2. Top models examining apparent nest success in Ross's (n = 10,269) and snow (n = 9,590) geese nests at the Karrak Lake light goose colony, south of Queen Maud Gulf, Nunavut, Canada, from 1993 to 2008. Only the top ten models out of twenty nine are shown here, ranked by ascending ΔAIC. The percent deviance explained of the top model was 6.7% [a].

Number/Model[b]	AIC[c]	ΔAIC[d]	w_i^e	K[f]	Log L[g]
1 {Species, Population, RNID, ELI, HAB, Nests, WC, CS, Species*RNID, Species*ELI, Species*WC, Species*CS}	19026.59	0.00	0.36	24	-9489.29
2 {Species, Population, RNID, ELI, HAB, Nests, WC, CS, Species*RNID, Species*ELI, Species*CS}	19027.26	0.68	0.26	22	-9491.63
3 {Species, Year, RNID, ELI, HAB, Nests, WC, CS, Species*RNID, Species*ELI, Species*WC, Species*CS}	19028.95	2.36	0.11	24	-9490.47
4 {Species, Population, RNID, ELI, HAB, Nests, WC, CS, Species*RNID, Species*ELI, Species*WC, Species*CS, Species*Nests}	19029.10	2.52	0.10	26	-9488.55
5 {Species, Year, RNID, ELI, HAB, Nests, WC, CS, Species*RNID, Species*ELI, Species*CS}	19029.72	3.14	0.08	22	-9492.86
6 {Species, Year, RNID, ELI, HAB, Nests, WC, CS, Species*RNID, Species*ELI, Species*WC, Species*CS, Species*Nests}	19025.19	4.76	0.03	26	-9489.68
7 {Species, Population, RNID, ELI, HAB, Nests, WC, CS, Species*RNID, Species*ELI, Species*WC, Species*CS, Species*Nests, Species*Population}	19032.01	5.42	0.02	28	-9488.00
8 {Species, Fat, RNID, HAB, Nests, WC, CS, Species*Fat, Species*RNID, Species*CS}	19032.07	5.48	0.02	21	-9495.03
9 {Species, Fat, RNID, HAB, Nests, WC, CS, Species*Fat, Species*RNID, Species*CS, Species*Nests}	19033.37	6.78	0.01	23	-9493.68
10 {Species, Year, RNID, ELI, HAB, Nests, WC, CS, Species*RNID, Species*ELI, Species*WC, Species*CS, Species*Nests, Species*Year}	19035.11	8.52	0.00	28	-9489.55

[a] A measure analogous to the coefficient of determination (R^2) in least squares regression (Cameron and Windmeijer 1997).

[b] Model factors included Species, Population (number of individuals in breeding colony in a given year), RNID (timing of nesting relative to other females of the same species in the same year), HAB (categorical effect, habitat type nest is located in; birch, rock, heath, moss, sand, mixed, or exposed), Nests (number of nests in the 60 meter diameter plot in which the nest is located), CS (clutch size, number of eggs in the nest bowl), ELI (early-lateness index, difference between annual mean nest initiation and long-term average from 1991 to 2008), WC (mean windchill during nesting, ºC), Fat (annual index of abdominal fat from birds collected at arrival

onto the breeding colony for each species separately), Year (linear time trend) and * (asterisk, denotes interaction between variables; otherwise effects are additive).
[c] Akaike's Information Criterion.
[d] Difference in AIC values between the model with the lowest AIC value.
[e] Estimates of the likelihood of the model, given the data; normalized to sum to one (Burnham and Anderson 2002).
[f] Number of estimable parameters.
[g] Log-likelihood of the current model.

Table 5.3. Model averaged odds ratio estimates and 95% CLs from top models of a logistic regression analysis of putative factors influencing apparent nest success in Ross's and snow geese nesting at the Karrak Lake light goose colony, south of Queen Maud Gulf, Nunavut, Canada, 1993 to 2008. Odds ratios were obtained by exponentiating coefficients from the logistic regression analysis.

Effect	Odds ratio (95% CL)
Population[a]	0.80 (0.76, 0.86)
Year[b]	0.97 (0.96, 0.98)
RNID[c]	
Snow geese	1.02 (1.00, 1.03)
Ross's geese	0.98 (0.96, 1.00)
Species*RNID	0.96 (0.94, 0.98)
Nests[d]	
Snow geese	1.00 (1.00, 1.01)
Ross's geese	1.01 (1.00, 1.01)
Species*Nests	1.00 (1.00, 1.01)
WC[e]	
Snow geese	1.10 (1.06, 1.15)
Ross's geese	1.16 (1.09, 1.19)
Species*WC	1.05 (1.00, 1.06)
CS[f]	
Snow geese	1.53 (1.46, 1.61)
Ross's geese	1.93 (1.82, 2.06)
Species*CS	1.26 (1.17, 1.37)
ELI[g]	
Snow geese	0.95 (0.94, 0.97)
Ross's geese	1.02 (1.00, 1.03)
Species*ELI	1.07 (1.04, 1.09)

[a] Number of individuals in breeding colony in a given year.
[b] Linear trend through time.
[c] Timing of nesting relative to other females of the same species in the same year.
[d] Index of nesting density; number of nests in the 60 meter diameter plot.
[e] Mean annual windchill during nesting, ºC.
[f] Clutch size, number of eggs in the nest bowl.
[g] Early-lateness index, difference between annual mean nest initiation and long-term average from 1993 to 2008.

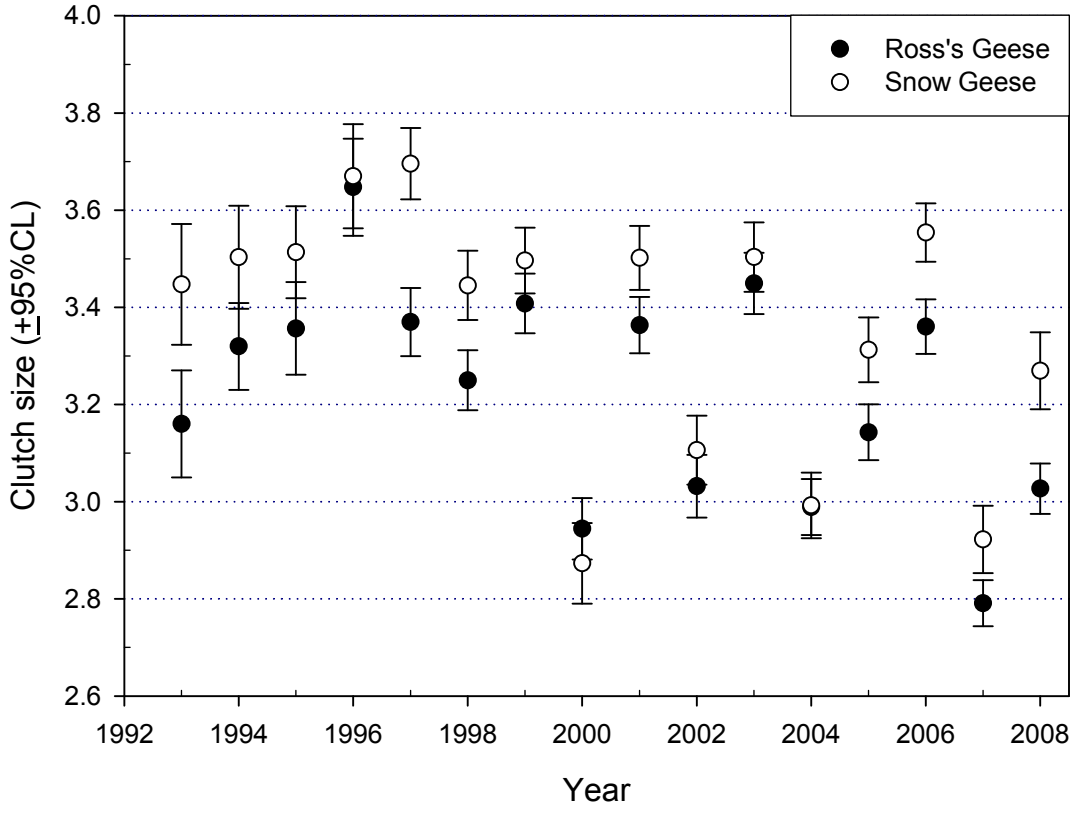


Figure 5.1. Annual mean estimates of clutch size (± 95% CL) for Ross's (*n* = 10,739) and snow (*n* = 10,270) geese nesting at the Karrak Lake light goose colony, south of Queen Maud Gulf, Nunavut, Canada, 1993 to 2008.

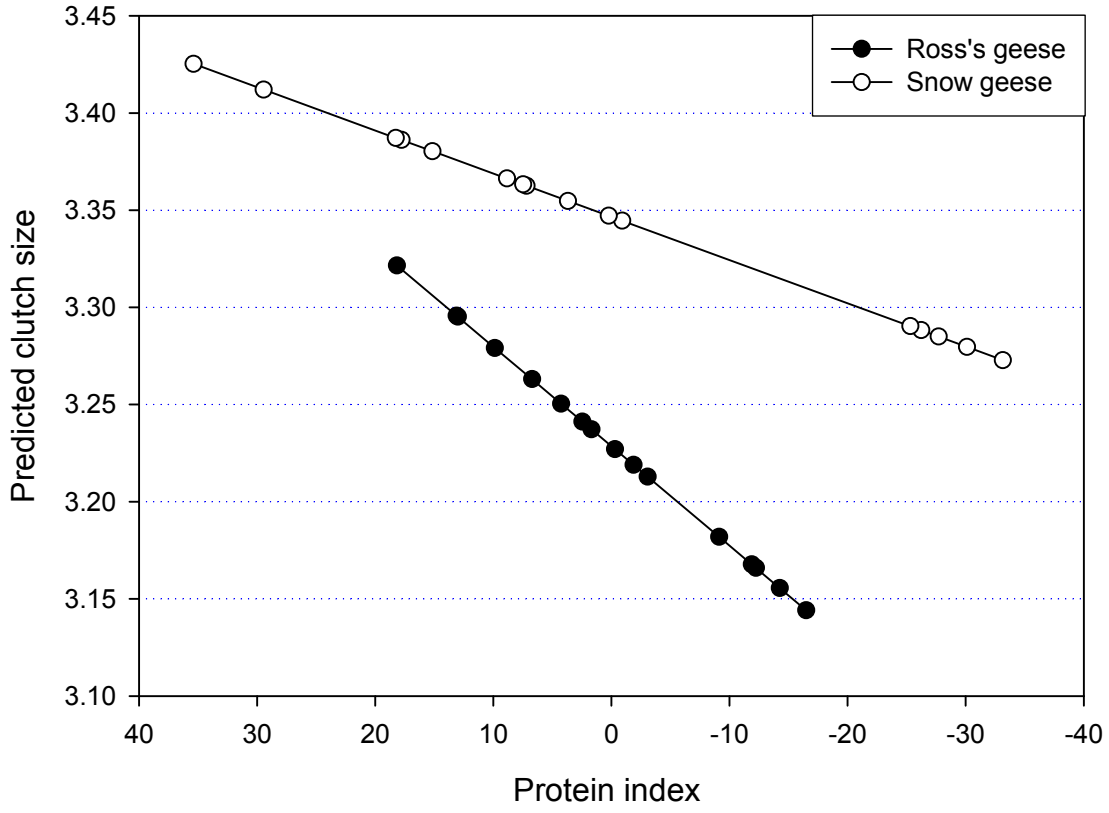


Figure 5.2. Predicted relationship between protein reserves and clutch size for Ross's and snow geese nesting at the Karrak Lake light goose colony, south of Queen Maud Gulf, Nunavut, Canada. Slope estimates are based on weighted model averaged estimates of ($\overline{\hat{\beta}}_{protein(snow)} =$ 0.0022 and $\overline{\hat{\beta}}_{protein(ross)} = 0.0051$) for snow and Ross's geese, respectively. The protein reserve index [one breast + one bone-free leg] was the difference between the annual mean protein mass and the long-term average from 1993 to 2008 from arriving birds collected at the breeding colony, done for each species separately.

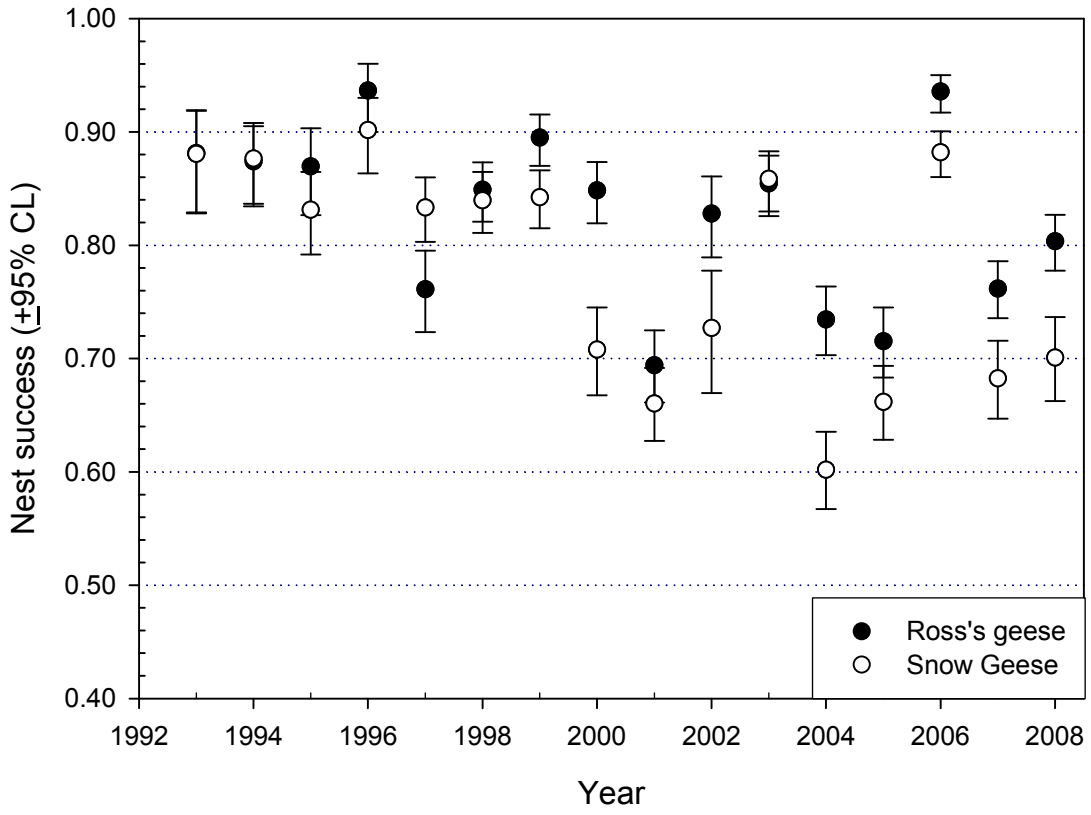
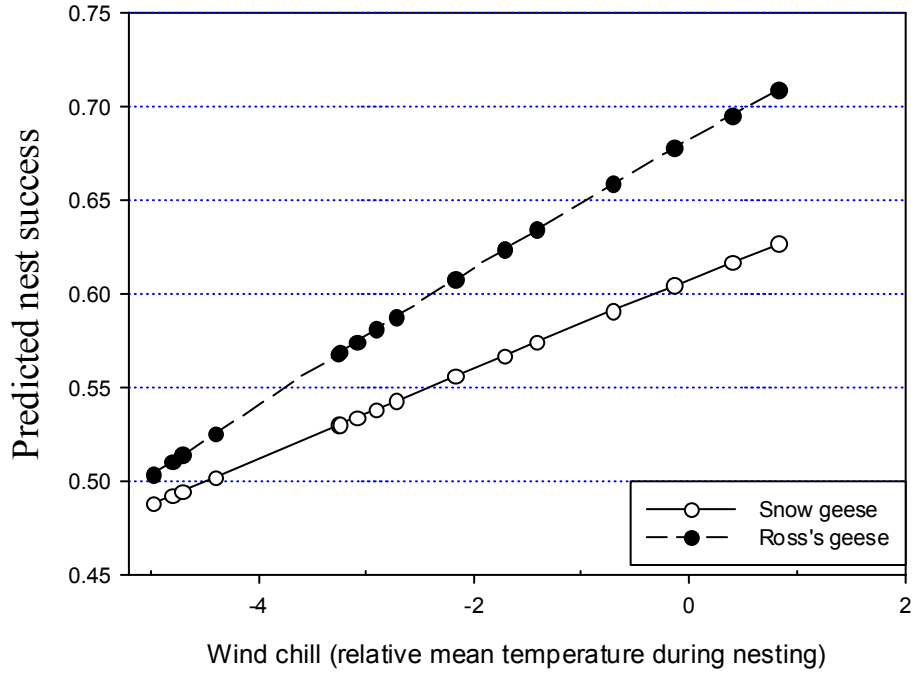


Figure 5.3. Annual mean estimates of nest success (± 95% CL) for Ross's (*n* = 10,269) and snow (*n* = 9,590) geese nesting at the Karrak Lake light goose colony, south of Queen Maud Gulf, Nunavut, Canada, 1993 to 2008.

a)



b)

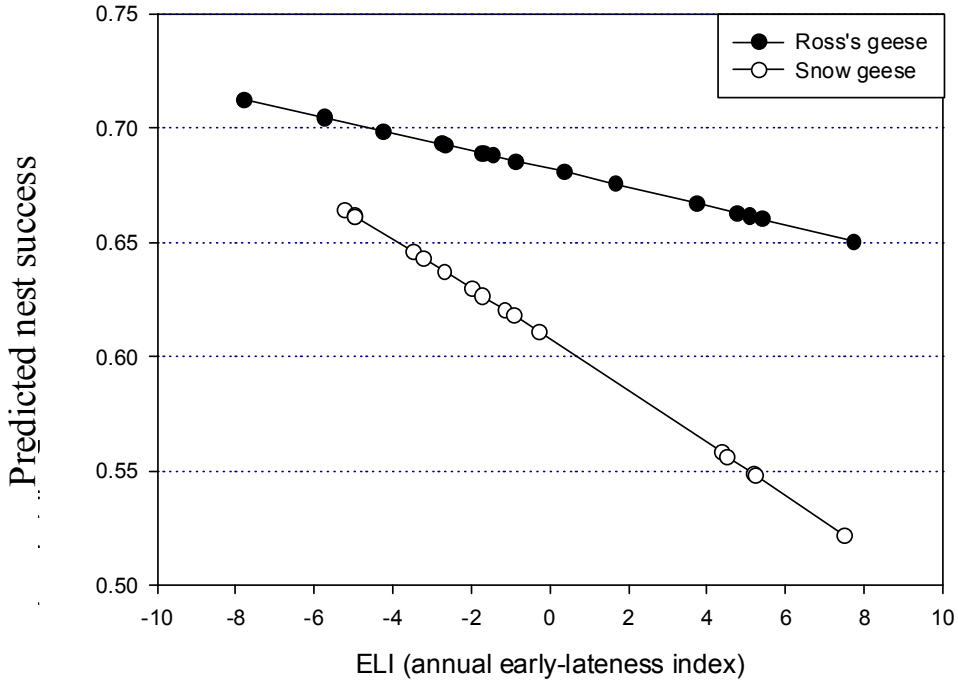


Figure 5.4. Predicted relationships of a) wind chill and b) early-lateness index on nest success of Ross's and snow geese nesting at the Karrak Lake light goose colony, south of Queen Maud Gulf, Nunavut, Canada. Slope estimates for windchill and early-lateness index are based on weighted model averaged estimates ($\overline{\hat{\beta}}_{WC(snow)} = 0.10$; $\overline{\hat{\beta}}_{WC(ross)} = 0.15$ and $\overline{\hat{\beta}}_{ELI(snow)} = -0.05$; $\overline{\hat{\beta}}_{ELI(ross)} = 0.01$) for snow and Ross's geese, respectively. Windchill was calculated as the mean windchill during nesting (ºC) and the early-lateness index was the difference between the annual mean nest initiation and long-term average from 1993 to 2008, done for each species separately.

6. COMPARATIVE SURVIVAL AND VULNERABILITY TO HUNTING OF JUVENILE ROSS'S AND LESSER SNOW GEESE

6.1 INTRODUCTION

In many long-lived species, adult survival has the greatest potential influence on population growth (Rockwell et al. 1997, Schmutz et al. 1997, Hoekman et al. 2002). Nevertheless, variation in recruitment can have important consequences for population change (Williams et al. 2002). Notably, recruitment in birds can show marked annual variation and, in turn, can become an important determinant of population growth rate (Nur & Sydeman 1999). Juvenile survival, i.e., survival between from fledging until one year later, is one of the many components of recruitment, and can be particularly important because it is a prime determinant of the proportion of new individuals entering a breeding population (Cooch et al. 2001, Reed et al. 2003). Using retrospective analysis, Cooch et al. (2001) found that variation in first year survival in lesser snow geese (*Chen caerulescens caerulescens*, hereafter snow geese) was more important to local population growth than adult survival. Juvenile survival can be modified by many interacting ecological, biological and physiological factors, though it is often linked to local environment conditions during development (Todd et al. 2003). Consequently, knowledge of factors that influence juvenile survival can reveal probable mechanisms of population change.

Breeding earlier in a season usually improves fitness. For instance, there is decreased survival among offspring produced later in a breeding season among fish (Schultz 1993), mammals (Iason 1989) and birds (Cooch 2002). In arctic-breeding geese, delayed nesting predictably reduces offspring survival because of decreased food availability and/or inclement weather (Sedinger and Raveling 1986, Cooch et al. 1991a, Schmutz et al. 2001). A large portion of juvenile mortality in geese likely occurs during their first migration (Owen and Black 1989, Francis et al. 1992, Menu et al. 2005). Individuals that are larger structurally and/or in better body condition are more apt to survive the energetically-expensive journey from arctic-breeding to fall-staging areas (Owen and Black 1989, Francis et al. 1992, Hill et al. 2003). Ultimately, ecological conditions on brood-rearing habitats are important to juvenile survival and future life history traits of goslings (i.e., fecundity and/or survival) (Sedinger et al. 1995, Lepage et al. 1999, Cooch 2002).

Life history traits of species are generally influenced by body size, to which potential for population growth is related (Peters 1983). Larger species typically have delayed sexual maturity, lower fecundity, and higher survival (Peters 1983). Among birds, and waterfowl in particular, the potential for recruitment to influence population trajectory appears to be greater for smaller species, which tend also to have lower probabilities of annual survival (Johnson et al. 1992, Saether et al. 1996, Ricklefs 2000). Environmental conditions also play a prominent role in shaping life history traits of species since body size is the cumulative result of size-dependent life history decisions and ecological conditions experienced during somatic growth (Stearns 1992). For example, animals that breed in environments with limited food resources, cold temperatures, and low digestibility of foods should evolve larger body size since it increases fasting endurance, potential for fat reserve storage, and heat retention (Fretwell 1972, Calder 1974, Peters 1983). While species that breed at higher latitudes should benefit from larger size, specific ecological conditions may confound this relationship; in particular, areas of severe resource limitation may negate the benefits of large body size especially during offspring growth (Blanckenhorn 2000).

Populations of arctic-breeding geese in North America have increased dramatically in recent years (Boyd et al. 1982, Alisauskas et al. 2009). Exponential increase has been attributed to agricultural food subsidies on winter and migration areas (Alisauskas et al. 1988, Bateman et al. 1988, Alisauskas and Ankney 1992), lower harvest rates (Francis et al. 1992), migrational refugia (Raveling 1978), and arctic climate amelioration (MacInnes et al. 1990). Consequently, large increases in size of several populations of North American geese have resulted in ecosystem-level increases in arctic herbivory (Batt 1997). For example, a breeding population of snow geese at La Pérouse Bay, Manitoba, has shown density dependence in recruitment through declines in food availability (Cooch et al. 1991b). At a large colony in the central Canadian arctic, two species of closely-related (99.7% similarity of DNA; Avise et al. 1992, Hebert et al. 2004), sympatric-breeding geese have shown different population trajectories. Populations of the larger-bodied snow goose grew at an annual rate of 16.7% from 1967 to 1988 while smaller-bodied Ross's geese (*Chen rossii*) populations grew at only 7.9% per year during the same time period (Kerbes 1994). Since 1988, Ross's geese have grown at 11.0% per year, a rate roughly double that shown by sympatric nesting snow geese (Alisauskas unpubl. data). Several mechanisms exist for this difference in population growth including interspecific differences in

immigration and emigration, and variation in annual survival of adults. However, age ratios (immature: adult) of harvested birds are twice as high for Ross's than snow geese and more importantly age ratios have declined in snow geese (Alisauskas 2002). This suggests a possible decrease in survival of juvenile snow geese, which may be due to density-dependent effects of reduced food availability being more severe on the larger-bodied species. For instance, Cooch et al. (1997) found increased mortality of fledgling males in comparison to females among snow geese during periods of severe resource limitation, even though males are only 2 to 6% larger. Ross's geese are small-bodied (~66% size of snow geese; mean mass at arrival to the nesting grounds was 1706 g versus 2522 g for Ross's and snow geese, respectively, R. Alisauskas unpubl. data) and may be closer to the minimum viable size for an arctic-breeding obligate avian herbivore. Relative to larger species, smaller herbivores may face a lower threshold at which forage conditions become poor, thus reducing the likelihood of incurring negative population consequences under similar environmental conditions (Sedinger et al. 1998, Blanckenhorn 2000).

I investigated differences in juvenile (first-year) survival between two closely-related species of arctic-breeding geese (Ross's and snow geese) that differ in body size, to better understand reasons for differences in rates of population change using 14 years of banding and recovery data. In addition, I was interested in estimation of the consequences of late nesting and the role that inclement weather plays in governing juvenile survival since little is known about how different sized congeners respond in the same but variable ecological conditions on their breeding grounds. My choices of ecological covariates (i.e., timing of nesting and inclement weather) are thought to represent significant ecological conditions experienced at hatch (growth) and at onset of southward migration. These species are closely related and breed sympatrically within large colonies, so I effectively controlled for phylogeny and varying ecological conditions. In turn, this allowed me to evaluate costs of lateness in reproduction and effects of weather and population size in assessing the importance of interspecific difference in body size to juvenile survival. I tested two mutually-exclusive hypotheses to explain differences in juvenile survival between species. The life history hypothesis predicts greater juvenile survival of the larger-bodied lesser snow goose since there is a general interspecific relationship between body size and survival among animals. Alternatively, the resource limitation hypothesis predicts greater first-year survival of Ross's geese because their absolute nutritional demands of attaining

adult body size are lower relative to snow geese, and thus are influenced less by effects of density-dependent reductions in food on brood-rearing habitats and delayed timing of reproduction. However, because Ross's geese are smaller they should experience lower survival compared to snow geese in years of inclement weather during migration.

6.2 METHODS

Geese were captured north of the largest known light goose (i.e., Ross's and snow geese in aggregate) colony within the Queen Maud Gulf Migratory Bird Sanctuary (QMGMBS) located at Karrak Lake (67° 14' N, 100° 15' W), Nunavut, Canada from 1991-2004. Number of light geese nesting at Karrak Lake has increased from ~17,000 individuals in 1967, to ~463,000 in 1993 (Kerbes 1994) and most recently to ~1.27 million in 2006 (Alisauskas unpubl. data). This colony alone is thought to constitute ~40% of the world's population of breeding Ross's geese, while the Sanctuary, which has numerous smaller colonies, contains ~95% of Ross's Geese (Ryder and Alisauskas 1995). Areas north of Karrak Lake constitute the primary brood-rearing habitat for both Ross's and snow geese produced at this colony (Slattery and Alisauskas 2007) and is composed of a heterogeneous mosaic of sedge meadows, tundra ponds, and rock outcrops (Ryder 1972, Didiuk and Ferguson 2005). Recently, Alisauskas et al. (2006a) found a large reduction in species richness and diversity of vegetation within the colony. Further, the colony is surrounded by a biodeterioration zone such that the protein content of graminoids increases farther from the periphery of the colony (Slattery 2000).

Geese were captured following methods described by Alisauskas and Lindberg (2002); geese were marked in early-August solely with CWS/USFWS metal leg bands, or with such leg bands and neck bands. I used data only from geese marked with leg bands to avoid biases in survival estimates caused by neck bands (Alisauskas and Lindberg 2002, Alisauskas et al. 2006b). Goslings were between 3-5 weeks of age at capture. Upon capture snow goose goslings are approximately 2-3 d older than Ross's goose goslings based on differences in nesting phenology (RTA unpubl. data). However, because Ross's goose goslings have a faster growth rate and grow to smaller final size (MacInnes et al. 1989) they are proportionately larger than snow goose goslings during capture. I obtained recovery information (date and location) of birds shot from the Bird Banding Laboratory of the U.S. Fish and Wildlife Service.

6.2.1 Ecological covariates

Timing of reproduction. - Seasonal delays in breeding reduce survival of juvenile geese (Sedinger et al. 1995, Cooch 2002). I used mean nest initiation dates calculated for each species as an index for timing of annual reproduction. Timing of nest initiation is governed by the disappearance of snow and exposure of nesting habitat; usually "late" years result when snow melt is delayed. Mean nest initiation date for each species was used as a cohort-level covariate to model timing of reproduction for each year (Fig. 6.1). I monitored between 98 and 884 nests per species and year from egg-laying to hatch from 1991 to 2004. For nests located during egg-laying, nest initiation date (NID) was calculated by subtracting the number of eggs in the nest, less one, from the date of discovery. NID of nests found during incubation were obtained by subtracting stage of embryonic development (Weller 1956) and clutch size (assuming 1 egg = 1.2 d for Ross's geese and 1.4 d for snow geese; Ryder and Alisauskas 1995, Mowbray et al. 2002) from the day the nest was found.

Weather. - Inclement weather on brood-rearing areas and at the onset of migration was predicted to reduce first-year survival of juveniles. I used weather data from the 3 nearest communities to obtain a weather index: Cambridge Bay (69˚ 06′ N, 105˚ 08′ W), Baker Lake (64˚ 18′ N, 95˚ 04′ W), and Gjoa Haven (68˚ 38′ N, 95˚ 51′ W). I used mean daily temperature and total precipitation for a seventeen day period after banding (i.e., 15 to 31 August). This allowed me to focus on the period at the onset of southward migration given most geese fledge in mid-August and are departing brood-rearing areas before 31 August. I believe that this approach permitted valid inference to be drawn about the relationship between survival and weather at latitudes that juvenile geese from Karrak Lake likely experienced on their first southward migration. I used principal component analysis (PCA, Proc PRINCOMP; SAS Institute 2008) to construct a weather index from mean daily temperature and total precipitation in each year (Cooch et al. 1991b). PCA of the correlation matrix resulted in a first principal component (PC1) with loadings of -0.70 for mean daily temperature (ºC) and 0.70 for total precipitation. PC1 accounted for 59% of the summed variance of the 2 input variables. Thus, PC1 was used as a weather index and positive PC1 values corresponded to warm and dry weather; this weather index was also used as a cohort-level covariate (Fig. 6.2).

6.2.2 Survival estimation

I used Brownie et al. (1985) band recovery models as implemented in Program MARK version 4.3 (White and Burnham 1999) to estimate probabilities of annual survival ($\hat{S}_i$) and recovery ($\hat{f}_i$) for the period of 1 year starting at the midpoint of the time of banding (early August) in year i. I pooled data by sex for each species in this analysis to reduce model complexity as survival does not appear to differ markedly between males and females (Alisauskas and Lindberg 2002, although see Drake 2006). To focus on juvenile survival (survival within the first year of life), I developed age-structured models to allow the transition of juvenile (hatch year) birds to adult (after hatch year) birds during the interval following banding. Data were formatted into matrices of annual recoveries for each species and age class, to focus on potential effects on survival and specific cohorts of juvenile geese.

I used the information theoretic approach based on Akaike's Information Criterion for selection of models from a candidate set developed from biological hypotheses that focused on juvenile survival probabilities (Burnham and Anderson 2002). I started with the most complex global model $\{S_{(a*s*t)} f_{(a*s*t)}\}$ without considering covariates (model notation follows Lebreton et al. 1992) that had 96 estimable parameters, wherein S_i and f_i varied by age [a: adult (A) vs. juvenile (J) age-classes], species (s: Ross's vs. Snow geese), and calendar year (t: time dependency). Goodness-of-fit was tested on the global model using the median $\hat{c}$ approach (White and Cooch 2006) to determine if the model met assumptions of homogeneity and independence. I subsequently adjusted the variance inflation factor, $\hat{c}$, to 1.058 (SE = 0.01) to adjust for lack of model fit (Burnham and Anderson 2002).

After I considered a global model, reduced parameter models were constructed that were progressively less complex. I maintained age structure in all models since I was interested primarily in juvenile survival probabilities. It is not possible to estimate juvenile survival and recovery probabilities without complimentary information on adult survival and recovery (Brownie et al. 1985); my primary interest was juvenile survival so I considered adult survival and recovery probabilities as nuisance parameters. I first tested for sources of variation in recovery probabilities and then used the best parameterization of recovery before proceeding with reduced parameter models of survival. Parameterization of temporal variation in my models included both annual effects (t) and linear time trends (T) over the course of the study. Such

linear changes in parameters over time may be consistent with links to density dependence of juvenile survival. I considered slopes of relationships between species, year and linear time trends to be different (*, interactive) and parallel (+, additive) (e.g., $\{S_{(A+s*T)*(J+s*T)}\ f_{(A+s+t)*(J+s+t)}\}$). To assess hypotheses regarding effects of NID and weather (W) on survival, as well as differences in survival between species (s), I modeled group-level covariates on *S*; subsequently, I estimated 95% CL (confidence limits) of slopes between *S* probabilities and n^{th} covariates of interest, denoted 95% CL ($\hat{\beta}_n$). I considered models with single or both covariates to test for an effect on juvenile survival. Annual effects of covariates on survival of these species were considered to be interactive (*, different) or additive (+, parallel) over time. Group covariates were included in the design matrix of program MARK, and were fitted to survival or recovery probabilities by linear constraints (logit scale). While there are *a priori* reasons for nonlinear effects in response variables, I did not consider them here.

The most parsimonious model was selected based on quasi-likelihood Akaike's Information Criterion ($QAIC_c$) corrected for small sample size and lack of fit due to overdispersion (Burnham and Anderson 2002). I used normalized Akaike weights (w_i) to evaluate likelihood of each model; w_i indicates the relative support for competing models in the candidate model set, and can be interpreted as the weight of evidence that a model is the most plausible, given the data and model set (Burnham and Anderson 2002). I summed w_i of all models (i.e., $\Sigma\ w_i$) with a given covariate and used this as a metric to assess importance of the covariate to survival (Burnham and Anderson 2002). To accommodate model selection uncertainty, I generated model-averaged parameter estimates (i.e., $\bar{\hat{S}}_i$, $\bar{\hat{f}}_i$, and $\bar{\hat{\beta}}_i$ of covariates) and unconditional standard errors from a confidence set of models from which the evidence ratio was ~0.125 (models 1 through 5; Table 6.1) (Burnham and Anderson 2002). Differential vulnerabilities between juvenile Ross's and snow geese were calculated as the quotient $\bar{\hat{f}}_{Ross's} / \bar{\hat{f}}_{Snow}$ (Alisauskas et al. 2006b). All analyses were done using SAS (SAS Institute 2008) or Program MARK (White and Burnham 1999).

6.3 RESULTS

I banded 50,919 Ross's and snow geese from 1991 to 2004, of which 17,942 were adult snow, 6,567 juvenile snow, 13,800 adult Ross's, and 12,610 juvenile Ross's geese. Of these, 1,305,

482, 819, and 772, respectively were shot, retrieved, and reported to the Bird Banding Laboratory. Mean nest initiation date varied annually, ranging between June 4 and June 19 (Fig 6.1); 1992, 2000, 2002, and 2004 were later years (i.e., $\geq$ 3d past mean NID) for Ross's geese and snow geese. Inclement weather (cold and wet) for 17 days after marking was pronounced in 1991, 1996, and 2000 (Fig. 6.2).

I considered 56 models with survival and recovery probabilities structured by species, age, and year; the covariates NID and W were assessed only for their potential effect on juvenile survival. The best supported model $\{S_{A[s+T]\ J[s*NID]}\ f_{(s*a)+t}\}$ had a model weight, $w_i = 0.35$ (Table 6.1, Model {1}). This model suggested a consistent difference in survival of adults, as well as a decline in adult survival for both species over the study; juvenile survival differed between species and was negatively related to NID, but the strength of this relationship was greater for Ross's geese than snow geese (Fig. 6.3). Recovery probability was best modeled with an interaction between species and age, which varied in an additive manner among years (Fig. 6.5). The second best model ($w_i = 0.25$, $\Delta QAIC_c = 0.68$) was very similar to the top-ranked model but instead included an interactive effect of T on adult survival such that adult Ross's geese experienced a steeper decline in survival than adult snow geese (Table 6.1, Model {2}). The third best model ($w_i = 0.14$, $\Delta QAIC_c = 1.79$) was very similar to the top-ranked model but instead included an additive effect of NID, rather than an interactive effect, on juvenile survival (Table 6.1, Model {3}). All other models had Akaike weights, $w_i \leq 0.10$, and $\Delta QAIC_c > 3.0$) and so had little support relative to the three best models. Models that included only effects of weather on juvenile survival were not well-supported.

From model-average estimates, juvenile survival was 29% higher for snow geese ($\overline{S}_t' =$ 0.484) than Ross's geese ($\overline{S}_t' = 0.376$, Table 6.2, Fig. 6.4). There was no evidence for a long-term decline in juvenile survival for either species; nonetheless there was considerable annual variation (Fig. 6.4). Estimates of recovery probability showed annual variation and increased over the course of the study (Fig. 6.5). Although models suggested support for an effect of species on recovery probability, the effect was equivocal ($\overline{\hat{\beta}}_{Specie} = -0.07$, 95% CL: -0.23, 0.09). However, though not statistically significant, juvenile Ross's geese were 1.07 times more vulnerable to harvest than juvenile snow geese (range: 1.068 in 1999 to 1.072 in 1993); predictably, juveniles were much more vulnerable to harvest by hunters than were adult geese

(Table 6.2, Fig. 6.5). There were no significant differences in survival or recovery probabilities between adult Ross's and snow geese (Figs. 6.4 and 6.5). Still, survival of adult Ross's geese ($\hat{\beta}_T$ = -0.05, 95% CL: -0.11, 0.01) appears to be decreasing at a faster rate than adult snow geese ($\hat{\beta}_T$ = -0.01, 95% CL: -0.06, 0.05), though estimates were imprecise (Fig. 6.4).

Nest initiation (Σw_i = 0.997) was more important to juvenile survival than was either an effect of weather (Σw_i = 0.2553) or a declining time trend (Σw_i = 0.007; Table 6.1). Juvenile Ross's and snow geese survived equally well in some years (e.g. 1994 and 1996; Fig. 6.3). However, survival in Ross's juveniles was more sensitive to delays in breeding ($\overline{\hat{\beta}}_{NID}$ = -0.09, 95% CL: -0.14, -0.04) than in snow juveniles (e.g., 2000) ($\overline{\hat{\beta}}_{NID}$ = -0.05, 95% CL: -0.11, 0.00) (Fig. 6.5); smaller-bodied Ross's geese were approximately twice as sensitive to delays in breeding compared to juvenile snow geese. Weather effects on juvenile survival were equivocal (Ross's geese $\hat{\beta}_W$ = 0.11, 95% CL: -0.12, 0.34 and snow geese $\hat{\beta}_W$ = 0.04, 95% CL: -0.26, 0.35), but suggested that survival in both species tended to increase with warmer/drier weather following marking. Finally, effects of a linear time trend (proxy for density dependence) on juvenile survival in either species were opposite than predicted ($\hat{\beta}_{T(ross's)}$ = 0.01, 95% CL: -0.02, 0.05; $\hat{\beta}_{T(snow)}$ = 0.02, 95% CL: -0.02, 0.07).

6.4 DISCUSSION

I did not find evidence for the resource limitation hypothesis (Slattery 2000, Alisauskas et al. 2006a); juvenile snow geese survived at higher rates than juvenile Ross's geese. This finding supports the life history hypothesis and thus is consistent with advantages of larger body size stemming from interspecific variation in life histories (Fretwell 1972, Peters 1983). An obvious source of mortality for geese is hunting but I don't believe that this was an important cause of the 29% interspecific difference in juvenile survival found here because this difference is far too high to be accountable to an interspecific difference in probability of recovery by hunters of only 7%. Thus, species differences cannot be attributed to differences in hunting mortality. Moreover, Alisauskas et al. (2006b) could find no relationship between harvest and survival among juvenile Ross's geese, despite a clear relationship found for adults; in fact, a weak positive relationship suggested that years of improved juvenile survival during first migration

may result in higher harvest of juveniles. Similarly, Francis et al. (1992) did not detect such a negative relationship in juvenile snow geese. Alisauskas et al. (2006b) speculated that inclement weather or poor nutrition on brood-rearing areas and perhaps during early fall migration was a more important source of juvenile mortality than was hunting. In accordance with speculated timing of major mortality in both species of juvenile geese, I also think that a major cause of the interspecific difference found in this study is expressed during the first southward migration (of 1800 km) (Francis et al. 1992, Slattery and Alisauskas 2002). Intraspecific studies have shown that structurally larger individuals and/or individuals in better body condition are more likely to survive because migration from arctic breeding to fall staging areas is energetically expensive (Owen and Black 1989, Francis et al. 1992, Slattery and Alisauskas 2002). I suspect that juvenile snow geese may survive at higher rates because of larger body size resulting in reductions in rate of heat loss, lower per capita metabolic expense, and improved starvation endurance (Calder 1974, Peters 1983, Futuyma 1998, Perrin 1998). On the other hand, juvenile Ross's geese likely have sufficient reserves during early migration but eventually may experience elevated mortality as inability to maintain energy or nutritional balance sets in, leading to debilitation and starvation. Additional design constraints associated with small body size, such as wing shape (Bowlin 2007) and smaller nutrient (protein and fat) stores (Calder 1974), may impinge further on juvenile survival during migration. However, it remains unknown whether most mortality occurred in the arctic before migration or during migration.

Delayed breeding within an extreme environment significantly reduced juvenile survival, a pattern more or less ubiquitous among arctic breeding birds (Cooke et al. 1995, van der Jeugd and Larsson 1998, Cooch 2002). I suggest that environmental factors in highly seasonal environments are the main reason for this effect since the arctic nesting season is shorter than at lower latitudes, and creates an important selection pressure. Lepage et al. (1999) suggested that the seasonal decline in fledgling success with later hatch date was more important than parental quality for greater snow geese (*C. caerulescens atlantica*) nesting in the eastern Canadian arctic. The proposed mechanism behind this decline is based on time constraints that lead to an inability by goslings to achieve sufficient somatic growth required for migration in late years (Sedinger and Flint 1991, Cooch et al. 1991a, Lesage and Gauthier 1998, Lepage et al. 1998). Growth is highly sensitive to variation in the quality and quantity of forage as offspring of arctic-breeding geese have particularly fast growth rates (MacInnes et al. 1989, Lesage and Gauthier 1997, Badzinski et al. 2002), and among the most

rapid in birds (Whitehead et al. 1990). Forage abundance and quality at the time of gosling growth decreased with later hatch, which subsequently reduced growth rates of later-hatched young (Sedinger and Raveling 1986, Cooch et al. 1991a, Lepage et al. 1998). Generally, as growing goslings acquire protein, it is partitioned into skeletal structure and then to soft tissues (Cooch et al. 1996). Consequently, in late years juvenile geese embark on their first southward migration with insufficient protein and fat reserves to complete migration (Williams et al. 1993, Cooke et. al. 1995, Sedinger et al. 1995, Slattery and Alisauskas 2002). In extreme circumstances, goslings that have not allocated adequate protein to breast muscles for migration may experience mortality either during early migration or on brood-rearing areas if there is insufficient time to achieve minimum fledge-size (Lesage and Gauthier 1998). Thus, the large inter-annual variation in juvenile survival likely results proximately from differences in weather and its ultimate influence on primary productivity and gosling growth in any given year, as well as from the interaction between poor weather and energy required for basic tissue maintenance.

Juvenile survival in smaller-bodied Ross's geese was twice as sensitive to delays in breeding compared to juvenile snow geese. Although Ross's geese generally nest later (2-3 d) than snow geese, their offspring fledge sooner (RTA unpubl. data; KLD pers. obs.) because goslings have a faster growth rate and grow to smaller final size (MacInnes et al. 1989). Presumably, delays in breeding by Ross's geese should then be effectively neutral when compared to snow geese. Perhaps juvenile Ross's geese face elevated constraints during late years because they possess higher growth constants than snow geese (MacInnes et al. 1989). Juvenile Ross's geese, by 3 weeks of age are 80% of adult size whereas juvenile snow geese by 5 weeks are still only 65% of adult size (Ryder and Alisauskas 1995, Mowbray et al. 2000). Ross's geese also have increased energy requirements such that they have increased rates of energy utilization (i.e., basal metabolic rate [BMR] is higher than in snow geese, 91.0 to 82.7 kcal/d) (Nagy 1987, Ryder and Alisauskas 1995, Mowbray et al. 2000). Consequently, harsh ecological conditions at arctic breeding sites should favor large body size (Fretwell 1972). However, environmental vicissitude can change the importance of body size in some years; I found that the disparity in juvenile survival between Ross's and snow geese increased with progressively later nest initiation dates suggesting that body size becomes increasingly important in later years (Cooch 2002).

I found no clear effect of inclement weather during a 17-day period following banding on juvenile survival in either species. Inclement weather can predictably decrease survival of juvenile geese either through hypothermia, starvation (snow covering food plants), or net energy loss (Johnson et al. 1992, Fortin et al. 2000, Menu et al. 2005). The cumulative effect of adverse weather can cause mortality, but the indirect effect may act to slow growth rates by decreasing metabolic activity (Ricklefs 1989). Weather events that precede migration may be significant because juveniles have little or no fat reserves (Lesage and Gauthier 1998) with which to meet energy demands in the face of reduced food availability. Lesage and Gauthier (1997) suggest that fat accumulation began after fledging in greater snow geese positing that juveniles could incur substantial mortality if they encountered inclement weather on their southward migration since they have little body fat. Body fat has twice the energy and water content per gram metabolized than protein or carbohydrate and thus becomes essential to migrants (Gill 1995).

There was no long-term decline in juvenile survival or recovery rates for either species, a result consistent with the absence of density dependence at this arctic colony. Francis et al. (1992) found a density-dependent decrease in juvenile survival and recovery probability in snow geese. Ultimately, they suggested that effects of density dependence were greatest during first migration, a time of high energy expenditure and little nutrient uptake. Nonetheless, there may have been density dependence in survival between hatch and my marking efforts, such that larger goslings tended to survive to be marked. For example, Slattery (2000) documented goslings captured farther from the colony were structurally larger and in better condition relative to those that dispersed shorter distances from the colony.

My results showed significant but predictable differences in vulnerabilities between juvenile and adult geese. Alisauskas et al. (2006b) suggested that recent increases in vulnerabilities (from 1960s to 2000s) of juvenile relative to adult Ross's geese were consistent with effects of density-dependent reduction in food such that juvenile geese may now arrive on the Canadian prairies in poorer condition. I found no significant interspecific differences in vulnerabilities between juvenile Ross's and snow geese, although Ross' geese were about 7% more vulnerable. Overall, I suspected snow geese to be more vulnerable to harvest if juveniles suffered from density dependence. In contrast, hunters have long perceived that juvenile Ross's geese were more vulnerable to harvest than juvenile snow geese (Dzubin 1965). I speculate that flock behavior and response may be different between species. For instance, juvenile Ross's

geese may fly lower into decoy spreads as they appear to be more inquisitive and less apprehensive than snow geese (Dzubin 1965). However, some of this perception may result from the fact that juvenile Ross's geese are ~2 times more vulnerable than adult Ross's geese (Alisauskas et al. 2006b). In general, vulnerabilities between juvenile Ross's and snow geese were consistently similar throughout the course of this study.

6.4.1 Management implications

Similar adult survival probabilities of adult Ross's and snow geese suggest differences in recruitment are influencing differences in local population growth. The Karrak Lake Ross's goose population has grown at a rate roughly double than the snow goose population since 1988 (Alisauskas and Rockwell 2001), this despite significantly lower first year survival than that of snow geese. Under the current scenario of decreasing nutritional value of forage plants in and around the colony (Slattery 2000, Alisauskas et al. 2006a), I predicted that juvenile snow geese would display diminished survival given their larger body size increases absolute nutritional demands. Clearly, other components of recruitment must be slowing local population growth of snow geese. Some populations of snow geese have experienced long term decreases in clutch size which have been attributed to decreasing food resources on staging areas (Cooch et al. 1989). Likewise, decreases in nutritional condition of arriving females may compromise their ability to successfully hatch nests. For example, poor condition birds may abandon or be unable to successfully defend nests from predator attacks (Ankney and MacInnes 1978, Thompson and Raveling 1987). Future investigations at this study site could focus on these components to better understand differences in population growth rate. I recommend continued research to monitor sources of variation in clutch size, nest success, as well as juvenile and adult survival of mid-continent populations of light geese, which in turn, will help to determine reasons for differences in population trajectories. Lastly, because I am also unsure of migration routes and stopover sites between central arctic breeding grounds and the Canadian prairies, I suggest managers consider the use of satellite transmitters on migrating geese. Additional research is needed to examine migration differences (i.e., stopover sites, timing and duration not only during fall but also spring migration) between Ross's and snow geese as well as condition of forage plants on staging areas.

Table 6.1. Model selection for estimation of survival, *S*, and recovery probability, *f*, of juvenile snow and Ross's geese banded from 1991 to 2004 at Karrak Lake, Nunavut. Only those of 55 models considered with Δ $QAIC_c \leq 16$ and the global model are shown, ranked by ascending $\Delta QAIC_c$. C-hat was 1.06 with a SE of 0.01.

Number/Model[a]	$QAIC_c$[b]	$\Delta QAIC_c$[c]	w_i[d]	K[e]	QDeviance[f]
1 {S A[s+T] * J[s*NID] f (s*a)+t}	32158.63	0.00	0.35	23	412.14
2 {S A[s*T] * J[s*NID] f (s*a)+t}	32159.31	0.68	0.25	24	410.82
3 {S A[s+T] * J[s+NID] f (s*a)+t}	32160.42	1.79	0.14	22	415.93
4 {S A[s+T] * J[s*NID*W] f (s*a)+t}	32161.65	3.02	0.08	25	411.15
5 {S A[s+T] * J[s+NID+W] f (s*a)+t}	32161.99	3.36	0.06	23	415.50
6 {S A[s+T] * J[s*NID+W] f (s*a)+t}	32162.05	3.42	0.06	24	413.55
7 {S A[s+T] * J[s+NID*W] f (s*a)+t}	32163.62	4.99	0.03	24	415.13
8 {S A[s+T] * J[NID] f (s*a)+t}	32164.48	5.85	0.02	22	420.00
9 {S A[s+T] * J[s*T*NID] f (s*a)+t}	32166.66	8.03	0.01	25	416.16
10 {S A[s+T] * J[s+W] f (s*a)+t}	32171.23	12.60	000	22	426.74
11 {S A[s+T] * J[s*T] f (s*a)+t}	32171.58	12.95	0.00	23	425.09
12 {S A[s+T] * J[s*W] f (s*a)+t}	32173.05	14.42	0.00	23	426.56
13 {S A[s*T] * J[s*T] f (s*a)+t}	32173.28	14.65	0.00	24	424.78
14 {S A[s*t] * J[s*t] f a*s*t} Global}	32247.38	88.75	0.00	96	354.55

[a] Models are denoted as additive (+) and/or multiplicative (*); factors included time dependency (t), linear trend with time (T), adult (A), juvenile (J), species (s), age (a), nest initiation date (NID), and weather on brood rearing areas after marking (W)..
[b] Quasi-likelihood Akaike's Information Criterion with small sample correction.
[c] Difference in $QAIC_c$ values between the model with the lowest $QAIC_c$ value.
[d] Estimates of the likelihood of the model, given the data; normalized to sum to one (Burnham and Anderson 2002).
[e] Number of estimable parameters.
[f] QDeviance is difference between – 2log-likelihood of the current model and that of the saturated model.

Table 6.2. Estimates of yearly and average ($\bar{x}$) survival ($\hat{S}$) and recovery ($\hat{f}$) rates for adult and juvenile snow and Ross's geese, respectively. Estimates are model averages from a confidence set of models and numbers in parentheses, below estimates, are associated SE's. Birds were banded in the Queen Maud Gulf Migratory Bird Sanctuary, Nunavut, Canada from 1991 to 2004.

	Adult Snow Geese		**Adult Ross's Geese**		**Juvenile Snow Geese**		**Juvenile Ross's Geese**	
Year	$\hat{S}$	$\hat{f}$	$\hat{S}$	$\hat{f}$	$\hat{S}$	$\hat{f}$	$\hat{S}$	$\hat{f}$
1991	0.879	0.008	0.872	0.008	0.450	0.014	0.348	0.015
	(0.021)	(0.002)	(0.024)	(0.002)	(0.052)	(0.003)	(0.038)	(0.004)
1992	0.877	0.012	0.869	0.011	0.440	0.021	0.258	0.022
	(0.018)	(0.002)	(0.022)	(0.002)	(0.045)	(0.004)	(0.035)	(0.004)
1993	0.875	0.005	0.866	0.004	0.482	0.008	0.315	0.009
	(0.016)	(0.001)	(0.020)	(0.001)	(0.038)	(0.003)	(0.030)	(0.003)
1994	0.873	0.009	0.862	0.008	0.540	0.015	0.532	0.016
	(0.014)	(0.002)	(0.018)	(0.002)	(0.045)	(0.004)	(0.051)	(0.003)
1995	0.871	0.015	0.859	0.014	0.502	0.026	0.404	0.028
	(0.012)	(0.002)	(0.016)	(0.002)	(0.040)	(0.005)	0.033)	(0.004)
1996	0.868	0.020	0.855	0.019	0.535	0.034	0.479	0.036
	(0.011)	(0.002)	(0.014)	(0.002)	(0.055)	(0.003)	(0.051)	(0.005)
1997	0.866	0.014	0.851	0.013	0.499	0.024	0.399	0.026
	(0.010)	(0.001)	(0.013)	(0.001)	(0.036)	(0.003)	(0.028)	(0.003)
1998	0.864	0.025	0.848	0.023	0.487	0.042	0.382	0.045
	(0.010)	(0.002)	(0.013)	(0.002)	(0.037)	(0.003)	(0.031)	(0.003)
1999	0.862	0.033	0.844	0.031	0.512	0.055	0.400	0.060
	(0.011)	(0.002)	(0.013)	(0.002)	(0.038)	(0.004)	(0.030)	(0.003)
2000	0.859	0.020	0.840	0.018	0.373	0.033	0.225	0.035
	(0.012)	(0.001)	(0.015)	(0.001)	(0.072)	(0.003)	(0.039)	(0.002)
2001	0.857	0.025	0.836	0.023	0.529	0.042	0.426	0.045
	(0.015)	(0.001)	(0.017)	(0.001)	(0.041)	(0.003)	(0.034)	(0.003)
2002	0.854	0.022	0.831	0.021	0.416	0.038	0.298	0.040
	(0.017)	(0.001)	(0.020)	(0.001)	(0.055)	(0.003)	(0.032)	(0.003)
2003	0.851	0.022	0.827	0.021	0.530	0.037	0.427	0.040
	(0.020)	(0.001)	(0.023)	(0.001)	(0.042)	(0.003)	(0.036)	(0.002)
2004	-	0.020	-	0.019	-	0.035	-	0.037
		(0.001)		(0.001)		(0.003)		(0.002)
$\bar{x}$	0.866	0.018	0.851	0.017	0.484	0.030	0.376	0.032
	(0.004)	(0.0004)	(0.005)	(0.0004)	(0.013)	(0.001)	(0.010)	(0.001)

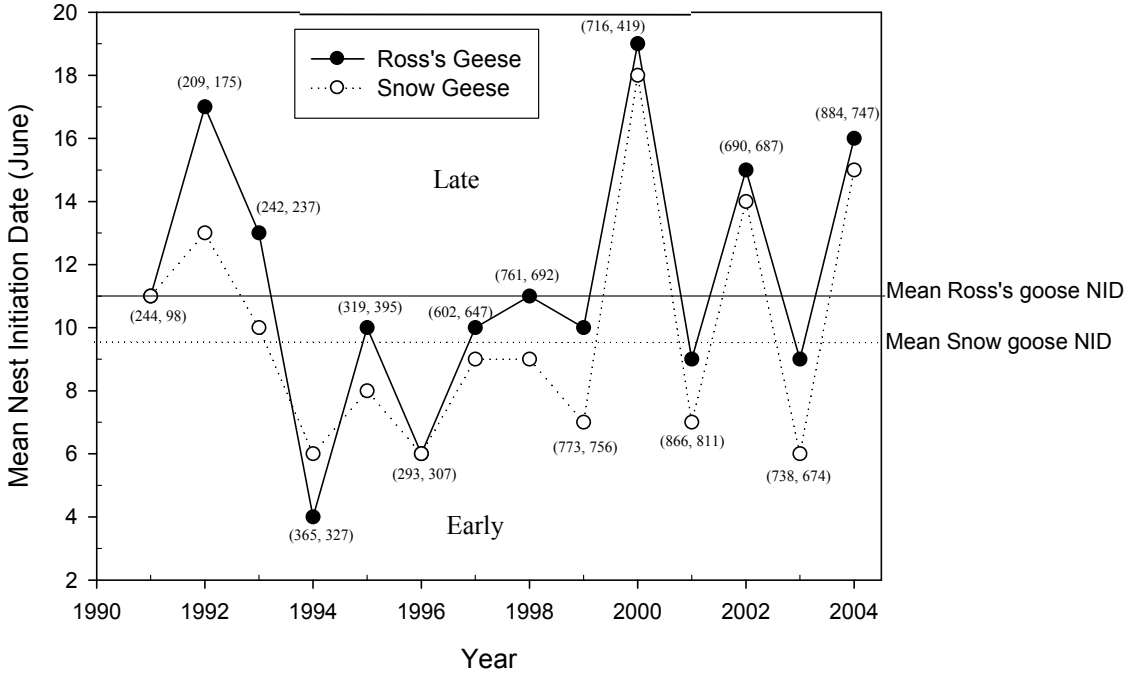


Figure 6.1. Nest initiation dates for Ross's and lesser snow goose nests at the Karrak Lake light goose colony, south of Queen Maud Gulf, Nunavut, Canada, from 1991 to 2004. Numbers in parentheses, in close proximity to data points, are sample sizes in a given year for Ross's and snow geese, respectively.

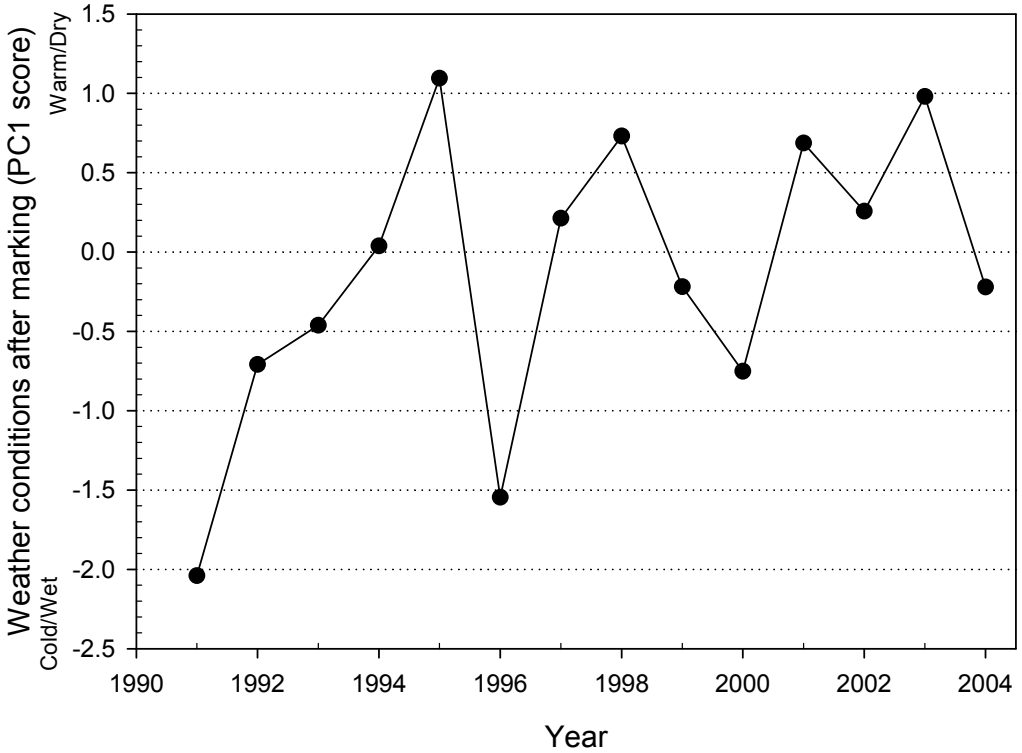


Figure 6.2. Weather conditions during a 17-day period after capture and marking of Ross's and snow geese, 1991 to 2004. The weather index was created using principal component analysis of total precipitation and mean daily temperature, and is meant to describe conditions experienced by goslings on brood-rearing areas before migration south.

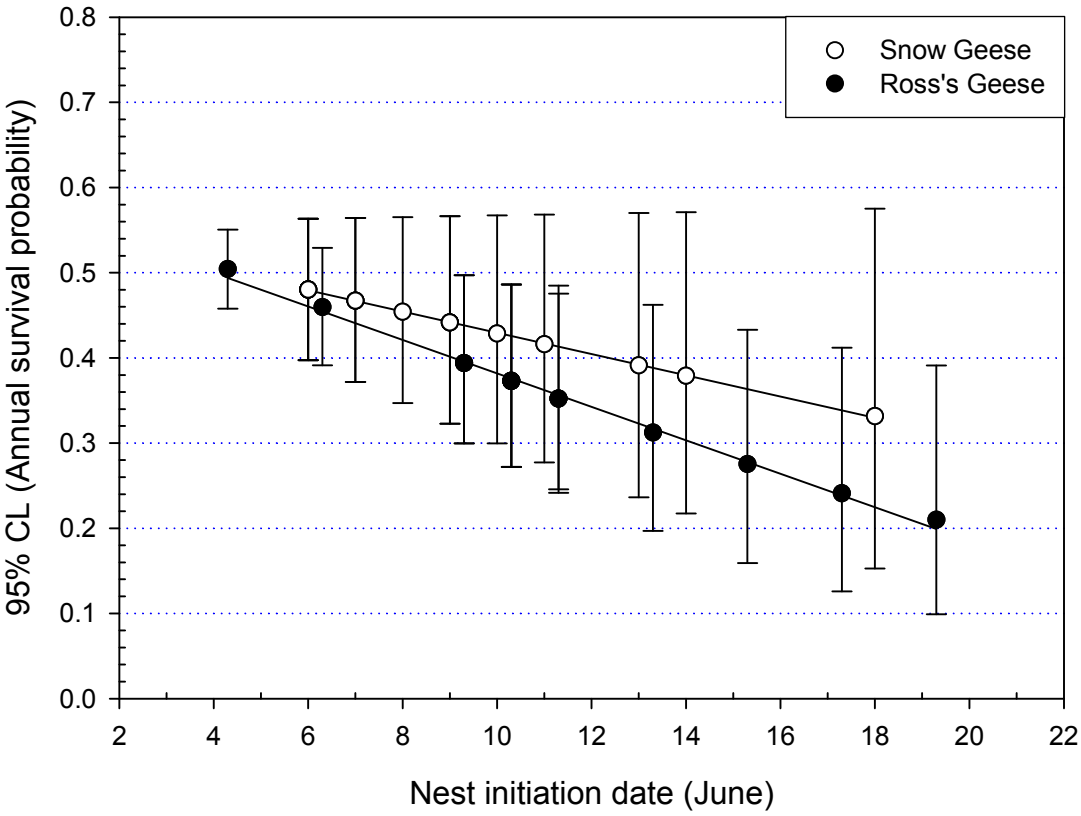


Figure 6.3. Relationship between Ross's and lesser snow goose juvenile survival probability for geese marked north of the Karrak Lake light goose colony, Nunavut, Canada, 1991 to 2003, and mean nest initiation date for Ross's ($\bar{\hat{\beta}}_{NID}$ = -0.09, 95% CL: -0.14, -0.04) and lesser snow ($\bar{\hat{\beta}}_{NID}$ = -0.05, 95% CL: -0.14, 0.00) geese. Survival estimates are model averages, back-transformed from the logit scale.

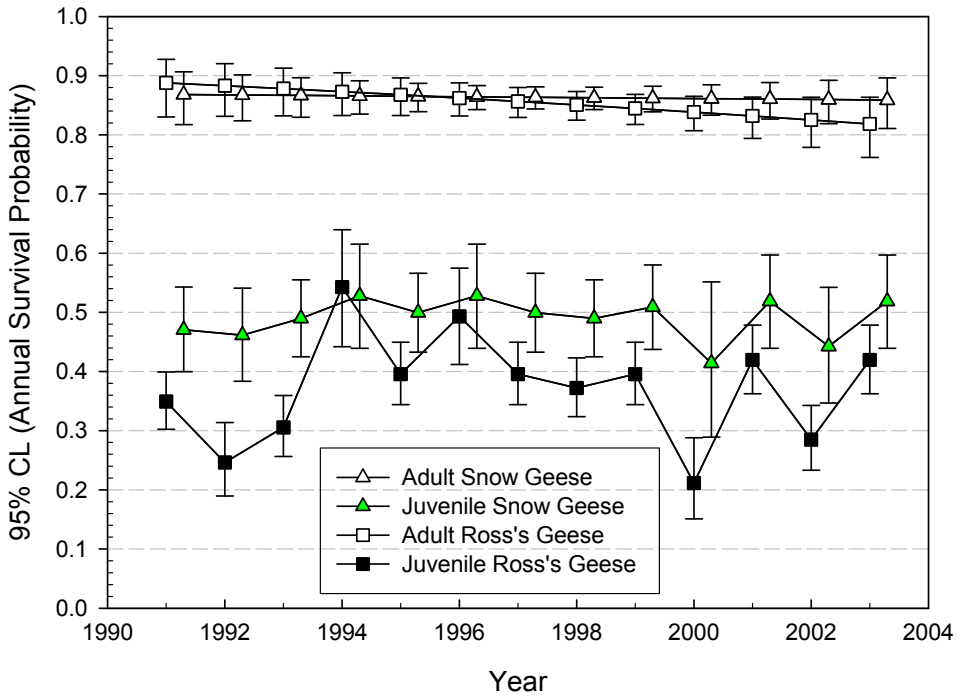


Figure 6.4. Model-averaged estimates of annual survival probability (± 95% CL) for juvenile and adult Ross's and lesser snow geese marked north of the Karrak Lake light goose colony, Nunavut, Canada, 1991 to 2003.

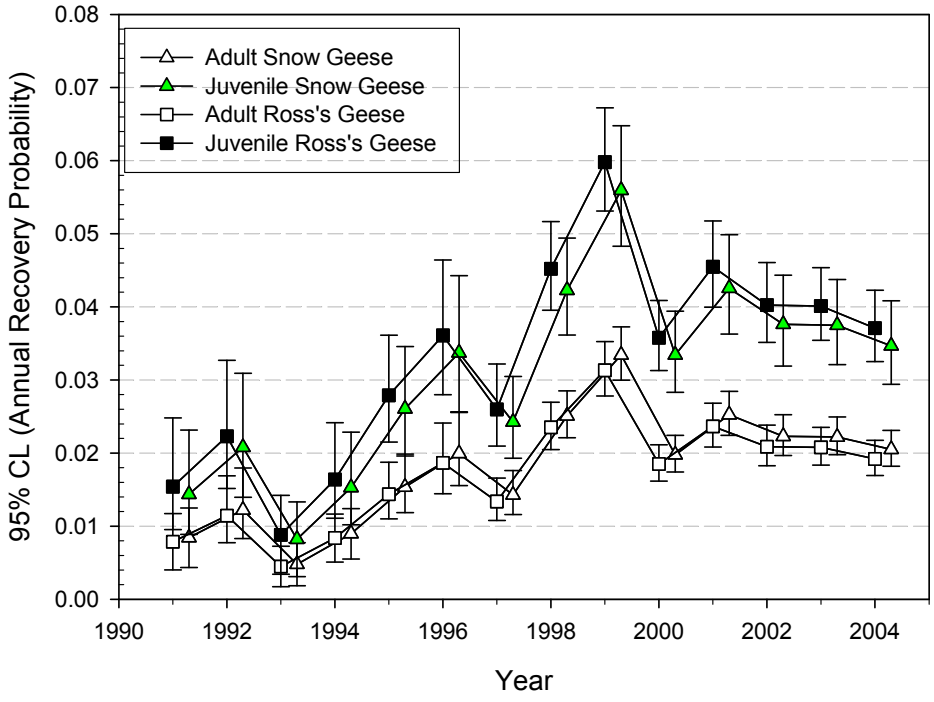


Figure 6.5. Model-averaged estimates of annual recovery probability (± 95% CL) for juvenile and adult Ross's and lesser snow geese marked north of the Karrak Lake light goose colony, Nunavut, Canada, 1991 to 2004.

7. SUMMARY AND SYNTHESIS

Local populations of smaller-bodied Ross's geese in the QMGBS in Canada's central arctic were growing at a rate approximately double that of populations of larger-bodied snow geese. Because the potential for recruitment to influence population trajectory is greater for smaller species, it was not unexpected that snow geese were experiencing slower rates of local population growth (Saether et al. 1996, Ricklefs 2000). However, when sympatric and ecologically similar species have widely differing reproductive success, they provide an opportunity to study how their adaptive responses to environmental conditions may be constrained by features of their life-history strategies. My main research objectives were to examine interspecific differences in three components of recruitment (clutch size, nest success, and juvenile survival) and identify ecological factors that influenced these components. I also examined interspecific variation in nutrient acquisition and allocation for reproduction by examining differences in spring nutrition during arrival onto the breeding colony and nutritional strategies used in clutch formation.

Information on differences in nutrient acquisition can reveal probable mechanisms of disparate population trajectories because of the significance of endogenous reserves to reproduction (clutch formation and incubation) in arctic geese (Ankney and MacInnes 1978, Arzel et al. 2006). In chapter 3, I examined changes in adult body size through time because of the importance of structural size to endogenous nutrient stores (Ankney and MacInnes 1978). There was some evidence that female geese of both species had decreased in body size through time as has been found at the local and superpopulation level in snow geese (Cooch et al. 1991b, Alisauskas 2002), although there was no evidence for a decline in structural size of males of either species. The apparent trend may have resulted from higher female philopatry to breeding areas (Drake and Alisauskas 2004, Alisauskas et al. 2011b). Consequently, if food restrictions at Karrak Lake influenced adult body size, then females with a higher likelihood of having been raised locally may have exhibited declines in body size (Anderson et al. 1992). The largest apparent influence on adult body size of arriving birds was spring severity. My results indicated that, in years with colder temperatures and more snow, body size of prospective breeders sampled in the colony was larger. This was likely the result of an absence of smaller birds arriving to breed in such years. Reed et al. (2004) surmised that spring snow cover and amount of stored endogenous reserves are important variables in arctic-goose breeding propensity.

In chapter 3, I also examined variation in spring nutrient acquisition. At the same time, snow geese displayed more rapid declines in protein and fat reserves over the course of the study relative to Ross's geese. These results are consistent with a long-term decline in ability to store nutrients during spring. Density dependence of spring nutrition has likely been brought about by intensive foraging on staging areas by snow geese. Bill morphology of snow geese allows foraging by grubbing below-ground plant parts (Ganter and Cooke 1996, Jefferies et al. 2004). Grubbing can weaken plants and cause cumulative damage with large increases in annual population size (Kerbes et al. 1990, Jefferies et al. 2004, Alisauskas et al. 2006a) thereby decreasing per capita forage availability and protein acquisition. Reductions in snow goose fat reserves likely occurred from decreased per capita food availability and increased energy expenditure from prospecting new food sources. Relative to the large reduction in spring nutrition by snow geese, Ross's geese may not have experienced large decreases in spring nutrition because their diminutive bill morphology and delayed northward spring migration may allow grazing of newly emerging vegetation on swards previously damaged by snow geese. However, because exact locations of northern staging areas remain unknown, Ross's geese may have affinities for different northern staging areas, which have not been denuded by snow geese.

Spring nutrient acquisition is extremely important during northward migration. During late spring migration before arriving on breeding colonies, geese generally acquire enough protein to lay an additional egg, maintain fat reserves, and satisfy energetic demands of migration and recrudescence of reproductive organs (Wypkema and Ankney 1979, Bon 1997). Density dependence on the ability to acquire proper spring nutrition may cause individuals to forego breeding altogether or delay breeding until birds acquire adequate levels of nutrients (Newton 2006). I found that significant delays in breeding had occurred, and these became acute more recently; Ross's and snow geese are now breeding 6.5 and 5.0 days later, respectively since 1991. Delays in breeding in highly seasonal arctic habitats could seriously impinge upon reproductive output via reductions in gosling or juvenile survival with delays in nesting (Chapter 6). Moreover, because delays in breeding predictably decrease fat reserves, reductions in reproductive output could also occur from decreased breeding probability, clutch size, and/or nest success.

In chapter 4, I examined interspecific differences in allocation of endogenous reserves to clutch formation. Body size is an integral component of organismal physiology and life history,

yet the underlying causes of life history variation brought about by differences in body size are not well understood (Ricklefs and Wikelski 2002). In general, physiological constraints may dictate tradeoffs in the acquisition and allocation of resources for reproduction and create differences in fecundity and survival (Nagy 1987, Stearns 1992, Ricklefs and Wikelski 2002). Relative to larger-bodied snow geese, smaller-bodied Ross's geese have an inefficient metabolism and smaller reserve carrying capacity (Calder 1972, Ankney and MacInnes 1978, Ankney 1984). Nonetheless, I found that Ross's geese allocated proportionally more endogenous reserves to clutch formation than did snow geese. Overall, larger-bodied snow geese arrived earlier to breed than Ross's geese, exploited more local vegetation for clutch formation on northern staging areas and utilized capital for incubation metabolism. By contrast, constraints of small size (i.e., relatively inefficient metabolism, absolutely smaller nutrient reserves) forced Ross's geese to use somatic reserves and concurrently assimilate local food plants (on the colony) to satisfy energetic demands of incubation (Gloutney et al. 2001). In total, Ross's geese lost a larger proportion of their body mass during breeding (arrival to hatch) compared to snow geese (38% vs. 32%), while controlling for respective masses of fresh clutches. In the end, I suggest that characterization of nutrient acquisition and allocation during reproduction (Chapters 3 and 4) has allowed insight of the life history variation between Ross's and snow geese.

In chapters 5 and 6, I examined the role of recruitment (i.e., variation in clutch sizes, nest success, and juvenile survival) in the interspecific divergence of population growth. Overall, snow geese had larger mean clutch sizes than Ross's geese. There was no large apparent decrease in clutch sizes through time in either species. However, clutch sizes declined with delays in breeding and decreasing protein reserves of arriving females. Clutch size in Ross's geese declined at a faster rate with decreasing protein reserves compared to snow geese. Smaller species carry absolutely less somatic reserve thus their clutch sizes are more sensitive to variation in protein reserves. Both species experienced decreased rates of nest success with increasing population size of the breeding colony. However, snow geese had lower probabilities of nest success compared to Ross's geese and the disparity increased with delays in breeding (i.e., from 5% to 13%). I suspect that differences in nest habitat selection and energy acquisition and allocation during incubation (Chapters 3 and 4) are prime determinants of this disparity because predation is likely minimal in large aggregations of nesting geese (McLandress 1983). Earlier arrival of snow geese forces use of upland, rockier areas of the colony, which contain

sparse vegetation for nest construction. Moreover, once arriving onto the breeding colony and initiating nesting, snow geese rely on endogenous reserves for clutch formation and incubation (Chapter 4). Consequently, any delays in breeding, which reduce limited endogenous reserves, decrease the female's ability to complete incubation (Ankney and MacInnes 1978, Raveling 1978). Likewise, nests of snow geese on exposed upland areas may fail because females initiate incubation recesses to forage which (1) may hinder embryo development, (2) cause death due to exposure to ambient conditions because inferior nest construction requires high nest attentiveness, or (3) render females unable to deter predation attempts (Thompson and Raveling 1987, McCracken et al. 1997). By contrast, later nest initiations of Ross's geese permits occupancy of lowland, better-vegetated areas that become accessible as the snow melts and which were previously unavailable to many snow geese. Subsequently, Ross's geese construct proportionally larger nests with greater insulative ability compared to snow geese, which likely provide a more suitable thermal environment for the developing embryos and permit lower incubation constancy (McCracken et al. 1997). Constraints of small-size and a capital-biased breeding strategy (partition endogenous reserves into clutch formation and lose absolutely more body mass from arrival to post-laying) compared to snow geese, cause Ross's geese to feed during incubation (Gloutney et al. 2001, Chapter 4). Subsequently, delays in breeding and associated decreases in fat reserves are likely not as detrimental to hatching success in Ross's geese because exclusive reliance on endogenous reserve is not feasible. Small size and overall lower energy requirements permit Ross's geese to assimilate local forage and concurrently use endogenous reserves to offset incubation metabolism (Thompson and Raveling 1987). In the end, diminished spring nutrition of snow geese may be a new mechanism for decreased reproductive success in years of delayed breeding because not only have snow geese experienced decreases in fat through time, they also arrive with progressively smaller fat reserves in years of delayed breeding (Chapter 3).

Lastly, juvenile snow geese survived at rates higher than juvenile Ross's geese, which was in agreement with life history theory (Peters 1983). I found no evidence of density dependence (i.e., a decline in juvenile survival over time). Delayed breeding in a highly seasonal environment significantly diminished juvenile survival of both species though juvenile Ross's geese were twice as sensitive as juvenile snow geese to delays in breeding. However, Ross's and snow geese had similar juvenile survival probabilities in early years though the disparity

increased with progressively later delays in breeding (i.e., up to 12%). Smaller body size of Ross's geese likely reduces survival compared to snow geese. Design constraints associated with small body size, such as smaller nutrient (protein and fat) stores (Calder 1974) likely impinge on juvenile survival during migration. Despite lower first-year survival, recruitment by Ross's geese may still be greater than that by snow geese because of earlier sexual maturity and/or greater nest success, especially in years of delayed breeding phenology (Chapter 5). However, because large differences in clutch size and nest success between species were not apparent, reductions in breeding probability, increased age of sexual maturity, and/or increased emigration by snow geese may contribute further to widening differences in local population trajectories.

Eberhardt (2002) predicted that populations under nutritional stress experience the following sequence of events: (1) decreased juvenile survival, (2) increased age of sexual maturity, (3) decreased reproductive rates, and (4) decreased adult survival. Because there was little change in adult survival and large interspecific differences in long-term trends in juvenile survival, clutch size and nest success were not apparent, components of recruitment that I did not consider such as age of sexual maturity and breeding probability may be diminishing reproductive rates of snow geese relative to Ross's geese. The age of sexual maturity (age at which female first breeds) and breeding probability (probability that a mature female breeds in a given year) influence the proportion of breeding individuals in the population in a given year, which has a profound effect on the number of offspring produced (Dobson and Oli 1999, Reed et al. 2004). Significant delays in breeding have been proposed to decrease breeding probability because delays in breeding predictably decrease endogenous reserves and/or snow inhibits nutrient acquisition needed for breeding (Prop and de Vries 1993, Reed et al. 2004). In chapter 3, I documented that snow geese arriving to breed have experienced substantial decreases in protein and fat reserves as well as significant delays in breeding. By contrast, non-breeders (geese that did not breed) are likely in comparably worse condition and thus could not breed for the reason that a nutrient reserve threshold required for breeding was not met. I suspect the proportion of adult snow geese that do not breed has increased substantially and thus is a major cause for the interspecific divergence of local population trajectory. Because nesting density of the breeding colony provides an index of annual variation in breeding probability (Reed et al. 2004), it is plausible that breeding probability has a large influence on annual differences in breeding population size at Karrak Lake. Subsequent large decreases in snow goose population size from

2006 to 2008 at Karrak Lake (597,421 to 311,676 birds) suggest decreased breeding propensity (Fig. 2.1).

Age of sexual maturity of subadult snow geese may also have increased at the Karrak Lake goose colony. Because young birds have less experience than older, more experienced conspecifics, it is reasonable to assume that young snow geese will likely not attempt to breed due to diminished per capita food conditions on staging areas thereby increasing age of sexual maturity. Life history theory predicts that snow geese, because of their larger body size, will have delayed sexual maturity compared to smaller-bodied Ross's geese. For example, two year old Brant geese, which are similar in size to Ross's geese, were found to have a breeding probability of 67% (Sedinger et al. 2001). In comparison, breeding probability of 2 year old snow geese ranged from ~23% to 53% (Cooch et al. 1999). In cyclic mammal populations, age of sexual maturity is the predominant factor influencing population growth rates; in years of high population density and low resource availability immature females delay reproduction and subsequently cause significant decreases in population growth (Oli and Dobson 1999). Accordingly, decreases in the proportion of breeders, either from decreased breeding probability and/or increased age of sexual maturity, in combination with reductions in clutch size and nest success have likely decreased snow goose productivity and caused disparate trends in local population trajectory.

Population regulation, through density dependence, is difficult to detect. Fowler et al. (2006) suggested detection of density dependence is predicated on experimental approaches and that conclusions regarding density dependence from observational data remain tenuous. Nevertheless, if time series data (of population size) indicate large increases through time and subsequent decreased growth rate (i.e., population regulation), ecologists can begin to understand the mechanism of regulation by examining demographic components (Bretagnolle et al. 2008). In general, previous studies about population regulation in arctic geese showed that increased density was associated with reduced juvenile survival (Francis et al. 1992, Sedinger et al. 1995). However, reduced recruitment may actually imply decreased reproductive effort at higher densities (Ebbinge 1985). Cooch et al. (1989) found a long-term reduction in clutch size in snow geese and surmised reductions in per capita food availability may be the cause. In this thesis, I did not find reductions in juvenile survival in either species, though density dependent mortality may have occurred during the gosling growth period such that only large, good condition

goslings were marked for the juvenile survival analysis. However, a novel finding, concerning snow geese, was significant reduction of spring nutrient stores used for breeding likely brought about by per capita reduction in food availability either from increased competition for food resources or severe cumulative forage damage (Chapter 3). Thus, reduction in breeding effort (decreases in clutch size and nest success, Chapter 5), brought about by diminished spring nutrition, is plausible given the importance of spring nutrient reserves to breeding geese (Ankney and MacInnes 1978). Still, substantial reduction in breeding effort likely occurs via decreased breeding probability (see above). Ultimately, life history traits of snow geese (e.g., protracted spring migration and early nest initiation on arctic breeding areas, absolutely higher energy requirements, and dependence upon endogenous reserves once reaching the breeding colony; Chapters 3 and 4) render their reproductive output more sensitive in areas with limited food resources (Blanckenhorn 2000).

In summary, this thesis examined interspecific differences in breeding strategies, acquisition of resources, and recruitment between two congeneric species that differ in body size to foster an understanding of disparate population trends. Because intraspecific variation in body size is the cumulative result of genetic and environmental influences (Boag and van Noordwijk 1987), adaptive responses to environmental conditions may be constrained by an organism's life history strategy (Harvey and Purvis 1999). In areas of resource limitation, life history traits of larger-bodied snow geese are likely not optimal. Body size should be important in areas of harsh climate such as arctic regions because larger size increases heat retention and fasting endurance, although larger body size necessarily increases daily energy requirements (Fretwell 1972, Blanckenhorn 2000). For instance, Piersma (2002) found that larger species of adult shorebirds incubating in the high arctic expended twice the amount of daily energy compared to smaller species, though smaller species were closer to their absolute maximum. Small body size of Ross's geese may produce an ideal life history schedule under resource limitation at this colony i.e., one that maximizes fitness relative to larger snow geese (Charlesworth 1980). Overall, life history characteristics of Ross's geese (e.g., absolutely lower energy requirements, higher reproductive effort [allocation of proportionately more endogenous reserves to reproduction], have a flexible breeding strategy [exploit local vegetation for incubation metabolism], an earlier age of sexual maturity, a shorter breeding cycle allowing delayed arrival and nest initiation on arctic breeding areas, and shorter time required by goslings to attain adult size), in addition to

their smaller bill morphology may allow exploitation of a wider niche space (i.e., one that includes marginal quality and low quantity vegetation) relative to snow geese.

LITERATURE CITED

Abraham, K. F., and R. L. Jefferies. 1997. High goose populations: causes, impacts, and implications. Pages 7-72 *in* Arctic ecosystems in peril: Report of the arctic goose habitat working group (B. D. J. Batt, ed). Arctic goose joint venture special publication. U. S. Fish and Wildlife Service, Washington, D. C. and Canadian Wildlife Service, Ottawa, Ontario.

Abrajano, T. A. Jr., D. E. Murphy, J. Fang, P., Comet, and J. M. Brooks. 1994. $^{13}C/^{12}C$ ratios in individual fatty acids of marine mytilids with and without bacterial symbionts. Organic Geochemistry 21:611–617.

Ackerman, J. T., J. M. Eadie, G. S. Yarris, D. L. Loughman, and M. R. McLandress. 2003. Cues for investment: nest desertion in response to partial clutch depredation in dabbling ducks. Animal Behavior 66:971–883.

Adams. T. S., and R. W. Sterner. 2000. The effect of dietary nitrogen content on trophic level ^{15}N enrichment. Limnology and Oceanography 45:601-607.

Afton, A. D. 1980. Factors affecting incubation rhythms of northern shovelers. Condor 82: 132-137.

Afton, A. D., and C. D. Ankney. 1991. Nutrient-reserve dynamics of breeding Lesser Scaup: A test of competing hypotheses. Condor 93:89-97.

Afton, A. D., and S. L. Paulus. 1992. Incubation and brood care. Pages 62-108 *in* Ecology and Management of Breeding Waterfowl (B. J. D. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu, Eds.). University of Minnesota Press, Minneapolis.

Agresti, A. 1996. An introduction to categorical data analysis. John Wiley and Sons Inc, New York, New York, USA.

Alisauskas, R. T. 1988. Nutrient reserves of lesser snow geese during winter and spring migration. Ph.D. Thesis, University of Western Ontario, London, Ontario.

Alisauskas, R. T. 1998. Winter range expansion and relationships between landscape and morphometrics of midcontinent lesser snow geese. Auk 115:851-862.

Alisauskas, R. T. 2002. Arctic climate, spring nutrition, and recruitment in midcontinent lesser snow geese. Journal of Wildlife Management 66:181-193.

Alisauskas, R. T., and C. D. Ankney. 1990. Body size and fecundity in Lesser Snow Geese. Auk 107: 440-443.

Alisauskas, R.T., and C. D. Ankney. 1992a. The cost of egg laying and its relationship to nutrient reserve in waterfowl. Pages 30 - 61 *in* Ecology and management of breeding waterfowl. (B. J. D. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu, Eds.). University of Minnesota Press, Minneapolis, Minnesota.

Alisauskas, R. T., and C.D. Ankney. 1992b. Spring habitat use and diets of mid-continent adult lesser snow geese. Journal of Wildlife Management 56:43-54.

Alisauskas R. T., and C. D. Ankney. 1994. Nutrition of breeding female Ruddy Ducks: the role of nutrient reserves. Condor 96:878-897.

Alisauskas, R. T., and K. A. Hobson. 1993. Determination of lesser snow goose diets and winter distribution using stable isotope analysis. Journal of Wildlife Management 57:49-54.

Alisauskas, R. T., J. W. Charlwood, and D. K. Kellett. 2006a. Vegetation correlates of the history and density of nesting by Ross's geese and lesser snow geese at Karrak Lake, Nunavut. Arctic 59:201-210.

Alisauskas, R. T., K. L. Drake, J. H. Caswell, and D. K. Kellett. 2011b. Movement and persistence by Ross's geese (*Chen rossii*) in Canada's arctic. Journal of Ornithology (*in press*).

Alisauskas, R. T., K. L. Drake, S. M. Slattery, and D. K. Kellett. 2006b. Neckbands, harvest, and survival of Ross's geese from Canada's central arctic. Journal of Wildlife Management 70:89-100.

Alisauskas, R. T., K. L. Drake, and J. D. Nichols. 2009. Filling a void: abundance estimation of North American populations of arctic geese using hunter recoveries. Environmental and Ecological Statistics 3:463-489.

Alisauskas, R. T., J. O. Leafloor, T. Moser, D. Caswell, D. K. Kellett. 2011a. Abundance of Ross's geese and midcontinent snow geese with recommendations for future monitoring. *in* B. D. J. Batt, editor, Arctic Ecosystems in Peril Reassessment (*in press*).

Alisauskas, R. T., and M. S. Lindberg. 2002. Effects of neckbands on survival and fidelity of White-fronted and Canada Geese captured as non-breeding adults. Journal of Applied Statistics 29:521-537.

Alisauskas, R. T., and R. F. Rockwell. 2001. Population dynamics of Ross's Geese. Pages 55-67 *in* The status of Ross's Geese. Arctic Goose Joint Venture Special Publication (T.J. Moser, Ed.). U.S. Fish and Wildlife Service, Washington, D.C., and Canadian Wildlife Service, Ottawa, Ontario.

Alisauskas, R. T., S. M. Slattery, J. P. Ryder, M. L. Gloutney, A. D. Afton, R. H. Kerbes, and M. R. Mclandress. 1998. Discrimination of Ross's and lesser snow goose eggs. Journal of Field Ornithology 69:647-653.

Allison, P. D. 1999. Logistic regression using the SAS system: theory and application. SAS Institute, Cary, North Carolina, pp. 1-288.

Anderson, M. G., J. R. Rhymer, and F. C. Rohwer. 1992. Philopatry, dispersal and the genetic structure of waterfowl populations. Pages 365-395 *in* Ecology and Management of Breeding Waterfowl (B. J. D. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu, Eds.). University of Minnesota Press, Minneapolis.

Ankney, C. D. 1977. Feeding and digestive organ size in breeding lesser snow geese. Auk 94:275-282.

Ankney, C. D. 1984. Nutrient reserve dynamics of breeding and molting brant. Auk 101:361 -370.

Ankney, C. D. 1996. An embarrassment of riches: too many geese. Journal of Wildlife Management 60:217-223.

Ankney, C. D., and C. D. MacInnes. 1978. Nutrient reserves and reproductive performance of female lesser snow geese. Auk 95:459-471.

Anteau, M. J., and A. D. Afton. 2009. Lipid reserves of lesser scaup (*Aythya affinis*) migrating across a large landscape are consistent with the "spring condition" hypothesis. Auk 126:873-883.

Anthony, T. W., P. L. Flint, and J. S. Sedinger. 1991. Arctic fox removal improves nest success of black brant. Wildlife Society Bulletin 19:176-184.

Armstrong, W. T. 1998. Predation and antipredator tactics of nesting black brant and lesser snow geese. Ph.D. Thesis, University of Saskatchewan, Saskatoon, Saskatchewan.

Arzel, C., J. Elmberg, and M. Guillemain. 2006. Ecology of spring-migrating Anatidae: a review. Journal of Ornithology 147:167-184.

Avise, J. C., R. T. Alisauskas, W. S. Nelson, and C. D. Ankney. 1992. Matriarchal population genetic structure in an avian species with female natal philopatry. Evolution 46:1084-1096.

Badyaev, A. V., and C. K. Ghalambor. 2001. Evolution of life histories along elevational gradients: trade-off between parental care and fecundity. Ecology 82:2948-2960.

Badzinski, S. S., C. D. Ankney, J. O. Leafloor, and K. F. Abraham. 2002. Growth and development of prefledging Canada geese and lesser snow geese: ecological adaptation or physiological constraint? Auk 119:221-227.

Baldwin, F. 2006. Factors influencing nest survival of cackling geese: the role of heterospecific geese. M.Sc. Thesis, University of Saskatchewan, Saskatoon, Saskatchewan.

Barry, T. W. 1962. Effect of late seasons on altantic black brant reproduction. Journal of Wildlife Management 26:19-26.

Bateman, H. A. T., T. Joanen, and C. D. Stuzenbaker. 1988. History and status of mid-continent Snow Geese on their Gulf Coast winter range. Pages 495-515 *in* Waterfowl in Winter. (M. W. Weller, Ed.) University of Minnesota Press, Minneapolis.

Batt, B. J. D., ed. 1997. Arctic ecosystems in peril: report to the Arctic Goose Habitat Working Group. Arctic Goose Joint Venture Special Publication. 120 pp. U. S. Fish and Wildlife Service, Washington D. C. and Canadian Wildlife Service, Ottawa, Ontario.

Bauer, S., P. Gienapp, and J. Madsen. 2008. The relevance of environmental conditions for departure decision changes en route in migrating geese. Ecology 89:1953-1960.

Begon, M., J. L. Harper, and C. R. Townsend. 1990. Ecology: Individuals, populations and communities. Blackwell Scientific Publications, Boston.

Bêty, J. G. Gauthier, and J.-F. Giroux. 2003. Body condition, migration and timing of reproduction in snow geese: a test of the condition-dependent model of optimal clutch size. American Naturalist 162:110-121.

Bêty, J., G. Gauthier, E. Korpimaki, and J. Giroux. 2002. Shared predators and indirect trophic interactions: lemming cycles and Arctic–nesting geese. Journal of Animal Ecology 71:88-98.

Bêty, J., J.-F. Giroux, and G. Gauthier. 2004. Individual variation in timing of migration: causes and reproductive consequences in greater snow geese (*Anser caerulescens atlanticus*). Behavioral Ecology and Sociobiology 57:1-8.

Blanckenhorn, W. U. 2000. The evolution of body size: what keeps organisms small? Quarterly Review of Biology 75:385-407.

Boag, P. T., and A. J. Van Noordwijk. 1987. The quantitative genetics of wild bird populations. Pages 45-78 *in* Avian genetics-its application to ecological and evolutionary theory (F. Cooke and P. A. Buckley, Eds.). London, Academic Press.

Bon, R. L. 1997. Spring nutritional ecology of migrating and breeding Ross' geese (*Chen rossii*). M.Sc. Thesis, University of Saskatchewan, Saskatoon, Saskatchewan.

Bond, J. C., D. Esler, and K. A. Hobson. 2007. Isotopic evidence for sources of nutrients allocated to clutch formation by Harlequin ducks. Condor 109:698-704.

Bonnet, X., D. Bradshaw, and R. Shine. 1998. Capital versus income breeding: an ectothermic perspective. Oikos 83:333-342.

Bourgeon, S., F. Criscuolo, F. Bertile, T. Raclot, G. W. Gabrielsen, and S. Massemin. 2006. Effects of clutch sizes and incubation stage on nest desertion in the female Common Eider Somateria mollissima nesting in the high Arctic. Polar Biology 29:358-363.

Bowlin, M. S. 2007. Sex, wingtip shape, and wing-loading predict arrival date at a stopover site in the swainson's thrush (*Catharus ustulatus*). Auk 124:1388-1396.

Boyd, H., G. E. J. Smith, and F. G. Cooch. 1982. The lesser snow goose of the Canadian arctic: their status during 1964-1979 and their management from 1981 to 1990. Canadian Wildlife Service Occasional Paper 46.

Bretagnolle, V., F. Mougeot, and J.-C. Thibault. 2008. Density dependence in recovering osprey population: demographic and behavioural processes. Journal of Animal Ecology 77:998-1007.

Brownie, C., D. R. Anderson, K. P. Burnham, and D. S. Robson. 1985. Statistical inference from band recovery data a handbook. 2nd edition. U.S. Fish and Wildlife Service, Resource Publication 156. Washington, D. C.

Bruggink, J. G., T. C. Tacha, J. C. Davies, and K. F. Abraham. 1994. Nesting and brood-rearing ecology of Mississippi Valley population of Canada geese. Wildlife Monographs 126:1-39.

Budeau, D. A., J. T. Ratti, and C. R. Ely. 1991. Energy dynamics, foraging ecology, and behavior of prenesting greater white-fronted geese. Journal of Wildlife Management 55:556-563.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information theoretic approach, 2nd Edition. Springer-Verlag, New York, Inc, pp. 1-488.

Calder, W. A., III. 1974. Consequences of body size for avian energetics. Pages 86-151 in Avian energetics (R.A. Paynter, Jr., Ed.). Nuttall Ornithological Club Publication 15.

Cameron, A. C., and F. A. G. Windmeijer. 1997. An R-squared measure of goodness of fit for some common nonlinear regression models. Journal of Economics 77:329-342.

Castillo, L. P., and K. A. Hatch. 2007. Fasting increases δ^{15}N-values in uric acid of *Anolis carolinensis* and *Uta stansburia* as measured by nondestructive sampling. Rapid Communications in Mass Spectrometry 21:4125-4128.

Caswell, H. 2000. Matrix population models. Second edition. Sinuar, Sunderland, Massachusetts.

Caswell, J. H. 2009. Population biology of Ross's geese at McConnell River, Nunavut. Ph.D. Thesis, University of Saskatchewan, Saskatoon, Saskatchewan.

Caut, S., E. Angulo, and F. Courchamp. 2008. Caution on isotopic model use for analyses of consumer diet. Canadian Journal of Zoology 86:438-445.

Charlesworth, B. 1980. Evolution in age structured populations. Cambridge University Press, Cambridge.

Cherel, Y., J.-P. Robin, and Y. Le Maho. 1988. Physiology and biochemistry of long-term fasting in birds. Canadian Journal of Zoology 66:159-166.

Choinière, L., and G. Gauthier. 1995. Energetics of reproduction in female and male greater snow geese. Oecologia 103:379-389.

Choudbury, S., and J. M. Black. 1994. Barnacle geese preferentially pair with familiar associates from early life. Animal Behavior 48:81-88.

Clutton-Brock, T. H., M. Major, and F. E. Guinness. 1985. Population regulation in male and female red deer. Journal of Animal Ecology 54:831-846.

Cooch, E. G. 2002. Fledging size and survival in snow geese: timing is everything (or is it?). Journal of Applied Statistics 29:143-162.

Cooch, E. G., R. L. Jefferies, R. F. Rockwell, and F. Cooke. 1993. Environmental change and the cost of philopatry: An example in the lesser snow goose. Oecologia 93:128-138.

Cooch, E.G., D. B. Lank, A. Dzubin, R.F. Rockwell, and F. Cooke. 1991a. Body size variation in Lesser Snow Geese: Environmental plasticity in gosling growth rates. Ecology 72:503-512.

Cooch, E. G., D. B. Lank, and F. Cooke. 1996. Intraseasonal variation in the development of sexual size dimorphism in a precocial bird: evidence from the lesser snow goose. Journal of Animal Ecology 65:439-450.

Cooch, E. G., D. B. Lank, R. F. Rockwell, and F. Cooke. 1989. Long-term decline in fecundity in a snow goose population: evidence for density dependence? Journal of Animal Ecology 58:711-726.

Cooch, E. G., D. B. Lank, R. F. Rockwell, and F. Cooke. 1991b. Long-term decline in body size in a Snow Goose population: Evidence of environmental degradation. Journal of Animal Ecology 60:483-496.

Cooch, E. G., D. B. Lank, R. F. Rockwell, and F. Cooke. 1992. Is there a positive relationship between body size and fecundity in lesser snow geese? Auk 109:667-673.

Cooch, E., D. Lank, R. Robertson, and F. Cooke. 1997. Effects of parental age and environmental change on offspring sex ratio in a precocial bird. Journal of Animal Ecology 66:189-202.

Cooch, E. G., D. B. Lank, R. F. Rockwell, and F. Cooke. 1999. Body size and age of recruitment in Snow Geese *Anser c. caerulescens*. Bird Study 46S:112-119.

Cooch, E. G., R. F. Rockwell, and S. Brault. 2001. Retrospective analysis of demographic responses to environmental change: a lesser snow goose example. Ecological Monographs 71:377-400.

Cooke, F., C. S. Findlay, and R. F. Rockwell. 1984. Recruitment and the timing of reproduction in Lesser Snow Geese. Auk 101:451-458.

Cooke, F., R. F. Rockwell, and D. B. Lank. 1995. The Snow Geese of La Pérouse Bay: Natural selection in the wild. Oxford University Press, Oxford.

Cottam. M., D. Houston, G. Lobley, and I. Hamilton. 2002. The use of muscle protein for egg production in zebra finch *Taenioipygia guttata*. Ibis 144:210-217.

Cowardin, L. M., and R. J. Blohm. 1992. Breeding population inventories and measures of recruitment. Pages 423-445 *in* Ecology and management of breeding waterfowl. (B. J. D. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu, Eds.). University of Minnesota Press, Minneapolis, Minnesota.

Croft, B. 1999. Nutrient reserves of small canada geese (*Branta canadensis hutchinsii*) nesting in the central Canadian Arctic. M.Sc. Thesis, University of Saskatchewan, Saskatoon, Saskatchewan.

Dalerum, F., and A. Angerbjörn. 2005. Resolving temporal variation in vertebrate diets using naturally occurring stable isotopes. Oecologia 144:647–658.

DeNiro, M., and S. Epstein. 1977. Mechanism of carbon isotope fractionation associated with lipid synthesis. Science 197:261–263.

DeVink, J.-M. 2007. Comparative reproductive energetics and selenium toxicology in three boreal-breeding waterfowl species. Ph.D. Thesis, University of Saskatchewan, Saskatoon, Saskatchewan.

DeVink, J.-M., R. G. Clark, S. M. Slattery, and D. L. Trauger. 2008. Are late-spring boreal lesser scaup (*Aythya affinis*) in poor body condition? Auk 125:291–298.

Didiuk, A. B., and R. S. Ferguson. 2005. Land cover mapping of Queen Maud Gulf Migratory Bird Sanctuary, Nunavut. Canadian Wildlife Service Occasional Paper 111:1-36.

Dobson, F. S., and M. K. Oli. 2007. Fast and slow life histories of mammals. Ecoscience 14:292-297.

Dobush, G. R. 1986. The accumulation of nutrient reserves and their contribution to reproductive success in the white-winged scoter. M.Sc. Thesis, University of Guelph, Ontario.

Doherty, P. F., J. D. Nichols, J. Tautin, J. F. Voelzer, G. W. Smith, D. S. Benning, V. R. Bentley, J. K. Bidwell, K. S. Bollinger, A. R. Bradza, E. K. Buelna, J. R. Goldsberry, R. J. King, F. H. Roetker, J. W. Solberg, P. P. Thorpe, and J. S. Wortham. 2002. Sources of variation in breeding-ground fidelity of mallards (*Anas platyrhynchos*). Behavioral Ecology 13:543-550.

Drake, K. L. 2006. The role of dispersal in population dynamics of breeding Ross's geese. Ph.D. Thesis, University of Saskatchewan, Saskatoon, Saskatchewan.

Drake, K. L., and R. T. Alisauskas. 2004. Breeding dispersal by Ross's geese in the Queen Maud Gulf metapopulation. Animal Biodiversity and Conservation 27.1:331-341.

Drent, R. H., and S. Daan. 1980. The prudent parent: energetic adjustments in avian breeding. Ardea 68:225-252.

Drent, R., B. Ebbinge, and B. Weijand. 1978. Balancing the energy budget of arctic-breeding geese throughout the annual cycle; a progress report. Verhandlungen der Ornithologischen Gesellschaft Bayerns 23:239–264.

Drent, R. H., A. D. Fox, and J. Stahl. 2006. Travelling to breed. Journal of Ornithology 147:122-134.

Drent, R. H., G. Eichhorn, A. Flagstad, A. J. Van der Graaf, K. E. Litvin, and J. Stahl. 2007. Migratory connectivity in arctic geese: spring stopovers are the weak links in meeting targets for breeding. Journal of Ornithology 148:S501-S514.

Dunn, E. H., and C. D. MacInnes. 1987. Geographic variation in clutch size and body size of Canada geese. Journal of Field Ornithology 58:355–371.

Dzubin, A. 1965. A study of migrating Ross's Geese in western Saskatchewan. Condor 67:511–534.

Dzus, E. H., and R. G. Clark. 1998. Brood survival and recruitment of mallards in relation to wetland density and hatching date. Auk 115:311-318.

Ebbinge, B. S. 1985. Factors determining the population size of Arctic-breeding geese, wintering in western Europe. Ardea 73:121-128.

Ebbinge, B. S., and B. Spaans. 1995. The importance of body reserves accumulated in spring staging areas in the temperate zone for breeding in dark-bellied Brent Geese *Branta b. bernicula* in the high arctic. Journal of Avian Biology 26:105-113.

Eberhardt, L. L. 2002. A paradigm for population analysis of long-lived vertebrates. Ecology 83:2841-2854.

Ely, C. R., and D. G. Raveling. 1984. Breeding biology of Pacific White-fronted Geese. Journal of Wildlife Management 48:823-837.

Ericsson, G, J. P. Ball, and K. Danell. 2002. Body mass of moose calves along an altitudinal gradient. Journal of Wildlife Management 66:91-97.

Fantle, M. S., A. I. Dittel, S. M. Schwalm, C. E. Epifanio, and M. L. Fogel. 1999. A food web analysis of the juvenile blue crab, *Callinectes sapidus*, using stable isotopes in whole animals and individual amino acids. Oecologia 120:416-426.

Felicetti, L. A., C. C. Schwartz, R. O. Rye, M. A. Haroldson, K. A. Gunther, D. L. Phillips, and C. T. Robbins. 2003. Use of sulfur and nitrogen stable isotopes to determine the importance of whitebark pine nuts to Yellowstone grizzly bears. Canadian Journal of Zoology 81:763-770.

Fèret, M., G. Gauthier, A. Bechet, J. F. Giroux, and K. A. Hobson. 2003. Effect of a spring hunt on nutrient storage by greater snow geese in southern Quebec. Journal of Wildlife Management 67:796-807.

Findlay, C. S., and F. Cooke. 1983. Genetic and environmental components of clutch size variance in a wild population of Lesser Snow Geese (*Chen caerulescens caerulescens*). Evolution 37:724-734.

Flint, P. L., and J. B. Grand. 1996. Nesting success of Northern Pintails on the coastal Yukon Kuskokwim Delta, Alaska. Condor 98:54-60.

Focken, U., and K. Becker. 1998. Metabolic fractionation of stable carbon isotopes: implications of different proximate compositions for studies of the aquatic food webs using $\delta^{13}C$ data. Oecologia 115:337-343.

Fortin, D., G. Gauthier, and J. Larochelle. 2000. Body temperature and resting behavior of greater snow goose goslings in the high arctic. Condor 102:163-171.

Fowler, N. L., R. D. Overath, and C. M. Pease. 2006. Detection of density dependence requires density manipulations and calculations of λ. Ecology 87:655-664.

Francis, C. M., M. H. Richards, F. Cooke, and R. F. Rockwell. 1992. Long-term changes in survival rates of Lesser Snow Goose. Ecology 73:1346-1362.

Fretwell, S. D. 1972. Populations in a seasonal environment. Princeton University Press, Princeton, New Jersey.

Futuyma, D. J. 1998. Evolutionary biology, 3rd edition. Sinauer Associates, Inc. Sunderland, Massachusetts.

Gannes, L. Z., C. Martinez del Rio, and P. Koch. 1998. Natural abundance variations in stable isotopes and their potential uses in animal physiological ecology. Comparative Biochemistry and Physiology A 119:725-737.

Ganter, B., and F. Cooke. 1996. Pre-incubation feeding activities and energy budgets of snow geese: can foods on the breeding grounds influence fecundity? Oecologia 106:153-165.

Gauthier, G. 1993. Feeding ecology of nesting greater snow geese. Journal of Wildlife Management 57:216-223.

Gauthier, G., J. Bêty, and K. A. Hobson. 2003. Are greater snow geese capital breeders? New evidence from a stable-isotope model. Ecology 84:3250-3264.

Gawlik, D. E., and R. D. Slack. 1996. Comparative foraging behavior of sympatric snow geese, greater white-fronted geese, and canada geese during the non-breeding season. The Wilson Bulletin 108:154-159.

Gill, F. B. 1995. Ornithology 2nd edition. W. H . Freeman and Company, New York.

Gloutney, M. L., R. T. Alisauskas, A. D. Afton, and S. M. Slattery. 2001. Foraging time and dietary intake by breeding Ross's and lesser snow geese. Oecologia 127:78-86.

Gloutney, M. L., R. T. Alisauskas, K. A. Hobson, and A. D. Afton. 1999. Use of supplemental food by breeding Ross's and lesser snow geese: evidence for variable anorexia. Auk 116:97-108.

Gloutney, M. L., and K. A. Hobson. 1998. Field preservation techniques for the analysis of stable-carbon and nitrogen isotope ratios in eggs. Journal of Field Ornithology 69:223-227.

Groscolas, R. 1986. The endocrine control of reproduction and molt in male and female Emperor (*Aptenodytes forsteri*) and Adélie (*Pygoscelis adeliae*) Penguins: I. Annual changes in plasma levels of gonadal steroids and luteinizing hormone. General and Comparative Endocrinology 62:43-53.

Hamann, J., and F. Cooke. 1987. Age effects on clutch size and laying dates of individual female lesser snow geese (*Anser caerulescens*) Ibis 129:527-532.

Hamann, J., and F. Cooke. 1989. Intra-seasonal decline of clutch size in lesser snow geese. Oecologia 79:83-90.

Hammer, B. T., M. L. Fogel, and T. C. Hoernig. 1998. Stable isotope ratios of fatty acids in seagrass and redhead ducks. Chemical Geology 152:29-41.

Harriman, V. B. 2006. Parasite-host interactions in an arctic goose colony. M.Sc. Thesis, University of Saskatchewan, Saskatoon, Saskatchewan.

Harriman, V. B., R. T. Alisauskas, and G. A. Wobeser. 2008. The case of the blood-covered egg: ectoparasite abundance in an arctic goose colony. Canadian Journal of Zoology 86:959-965.

Harvey, J. M. 1971. Factor affecting blue goose nesting success. Canadian Journal of Zoology 49:223-234.

Harvey, P. H., and A. Purvis. 1999. Understanding the ecological and evolutionary reasons for life history variation: mammals as a case study. Pages 232-248 *in* Advanced Ecological Theory: Principles and Applications. (J. McGlade, Ed.). Oxford, Blackwell Science.

Hebert, P. D. N., M.Y. Stoeckle, T. S. Zemlak, and C. M. Francis. 2004. Identification of birds through DNA barcodes. PloS Biology 2:1657-1663.

Heitmeyer, M. E., and L. H. Fredrickson. 1990. Fatty acid composition of wintering mallards in relation to nutrient use. Journal of Wildlife Management 54:54-61.

Heppell, S. S., H. Caswell, and L. B. Crowder. 2000. Life histories and elasticity patterns: perturbation analysis for species with minimal demographic data. Ecology 81:654-665.

Hik, D. S., and R. L. Jefferies. 1990. Increases in the net aboveground primary production of a salt marsh forage grass: a test of the predictions of the herbivore-optimization model. Journal of Ecology 78:180-195.

Hill, M. R. J., R. T. Alisauskas, C. D. Ankney, J. O. Leafloor. 2003. Influence of body size and condition on harvest and survival of juvenile Canada geese. Journal of Wildlife Management 67:530-541.

Hobson, K. A. 1995. Reconstructing avian diets using stable-carbon and nitrogen isotope analysis of egg components: patterns of isotopic fractionation and turnover. Condor 97: 752-762.

Hobson, K. A., R. T. Alisauskas, and R. G. Clark. 1993. Stable-nitrogen isotope enrichment in avian tissues due to fasting and nutritional stress: implications for isotopic analyses of diet. Condor 95:388–394

Hobson, K. A., L. Atwell, L. I. Wassenaar, and T. Yerkes. 2004. Estimating endogenous nutrient allocations to reproduction in Redhead ducks: a dual isotope approach using D and ^{13}C measurements of female and egg tissues. Functional Ecology 18:737–745

Hobson, K. A., and R.G. Clark. 1992. Assessing avian diets using stable isotopes I: turnover of ^{13}C in tissues. Condor 94:181-188.

Hoekman, S. T., L. S. Mills, D. W. Howerter, J. H. Devries, and I. J. Ball. 2002. Sensitivity analyses of the life cycle of midcontinent mallards. Journal of Wildlife Management 66:883-900.

Houston D. C., D. Donnan, and P. J. Jones. 1995. The source of the nutrients required for egg production in Zebra Finches *Poephila guttata*. Journal of Zoology London 235:469–483.

Iason, G. R. 1989. Growth and mortality in mountain hares: the effect of sex and date of birth. Oecologia 81:540-546.

Jackson, S. L., S. D. Hik, and R. F. Rockwell. 1988. The influence of nesting habitat on reproductive success of the lesser snow goose. Canadian Journal of Zoology 66:1699-1703.

Jefferies, R. L. 1988. Vegetational mosaic, plant-animal interaction, and resources for plant growth. Pages 341-369 *in* Plant Evolutionary Biology (L. Gottleib and S.K. Jain, Eds.). Chapman and Hall, New York.

Jefferies, R. L., R. F. Rockwell, and K. F. Abraham. 2004. The embarrassment of riches: agricultural food subsidies, high goose numbers, and loss of arctic wetlands – a continuing saga. Environmental Review 11:193-232.

Johnson, D. H., J. D. Nichols, and M. D. Schwartz. 1992. Population dynamics of breeding waterfowl. Pages 446-485 *in* Ecology and management of breeding waterfowl. (B. D. J. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu, Eds.). University of Minnesota Press, Minneapolis.

Johnston, D. W. 1973. Cytological and chemical adaptations of fat deposition in migratory birds. Condor 75:108–113.

Jönsson, K. I. 1997. Capital and income breeding as alternative tactics of resource use in reproduction. Oikos 78:57-66.

Jónsson, J. E., A. D. Afton, and R. T. Alisauskas. 2007. Does body size influence nest attendance? A comparison of Ross's geese (*Chen rossii*) and the larger, sympatric lesser snow geese (*Chen caerulescens caerulescens*). Journal of Ornithology 148:549-555.

Kendall, M. D., P. Ward, and S. Bacchus. 1973. A protein reserve in the pectoralis major muscle of *QueIea queIea.* Ibis 115:600-601.

Kerbes, R. H. 1994. Colonies and numbers of Ross's Geese and Lesser Snow Geese in the Queen Maud Gulf Migratory Bird Sanctuary. Canadian Wildlife Service Occasional Paper 81:1-47.

Kerbes, R. H., P. M. Kotanen, and R. L. Jefferies. 1990. Destruction of wetland habitats by lesser snow geese: a keystone species on the west coast of Hudson Bay. Journal of Applied Ecology 27:242-258.

Kirkwood, R., and G. Robertson.1997. The foraging ecology of female emperor penguins in winter. Ecological Monographs 67:155-176.

Klaassen, M. 2003. Relationships between migration and breeding strategies in arctic breeding birds. Pages 237 - 249 *in* Avian Migration. (P. Berthold, E. Gwinner, and E. Sonnenschein, Eds). Springer-Verlag, Berlin.

Klaassen, M., K. F. Abraham, R. L. Jefferies, and M. Vrtiska. 2006. Factors affecting the site of investment, and the reliance on savings for arctic breeders: the capital–income dichotomy revisited. Ardea 94:371–384.

Koch, P. L., and D. L. Phillips. 2002. Incorporating concentration dependence in stable isotope mixing models: a reply to Robbins, Hilderbrand and Farley (2002). Oecologia 133:14-18.

Krapu, G. L., and Reinecke, K. J. 1992. Foraging ecology and nutrition. Pages 1-29 *in* Ecology and management of breeding waterfowl. (B. J. D. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu, Eds.). University of Minnesota Press, Minneapolis, Minnesota.

Lack, D. 1954. The natural regulation of animal numbers. Oxford University Press.

Lack, D. 1968. Ecological adaptations for breeding birds. Methuen and Company, London.

Langin, K. M., D. R. Norris, T. K. Kyser, P. P. Marra, and L. M. Ratcliffe. 2006. Capital versus income breeding in a migratory passerine bird: evidence from stable carbon-isotopes.

Langvatn, R., S. D. Albon, T. Burkey, and T. H. Clutton- Brock. 1996. Climate, plant phenology and variation in age of first reproduction in a temperate herbivore. Journal of Animal Ecology 65:653–670.

Lank, D. B., P. Mineau, R. F. Rockwell, and F. Cooke. 1989. Intraspecific nest parasitism and extra-pair copulation in lesser snow geese. Animal Behavior 37:74-89.

Larsson, K., and P. Forslund. 1991. Environmentally induced morphological variation in the Barnacle goose, *Branta leucopsis*. Journal of Evolutionary Biology 4:619-636.

Larsson, K., and P. Forslund. 1992. Genetic and social inheritance of body size and egg size in the Barnacle Goose (*Branta leucopsis*). Evolution 46:235-244.

Larsson, K., H. P. Van Der Jeugd, I. T. Van Der Veen, and P. Forslund. 1998. Body size declines despite positive directional selection on heritable size traits in a barnacle goose population. Evolution 52:1169-1184.

Lebreton, J-D., K. P. Burnham, J. Clobert, and D. R. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. Ecological Monographs 62:67-118

Lecomte, N., V. Careau, G. Gauthier, and J.-F. Giroux. 2008. Predator behavior and predation risk in heterogeneous arctic environment. Journal of Animal Ecology 77:439-447.

Lepage, D., G. Gauthier, and S. Menu. 2000. Reproductive consequences of egg-laying decisions in snow geese. Journal of Animal Ecology 69:414-427.

Lessells, C. M. 1986. Brood size in Canada Geese: a manipulation experiment. Journal of Animal Ecology 55:669-689.

Le Maho, Y., H. Vu Van Kha, H. Koubi, G. Dewasmes, J. Girard, P. Ferre, and M. Cagnard. 1981. Body composition, energy expenditure, and plasma metabolites in long-term fasting geese. American Journal of Physiology 241:342-354.

LeSchack, C. R., A. D. Afton, and R. T. Alisauskas. 1998. Effects of male removal on female reproductive biology in Ross' and lesser snow geese. Wilson Bulletin 110:56-64.

Lepage, D., Gauthier, G., and A. Reed. 1998. Seasonal variation in growth of Greater Snow Goose goslings: The role of food supply. Oecologia 114:226-235.

Lepage, D., A. Desrochers, and G. Gauthier. 1999. Seasonal decline of growth and fledging success in Snow Geese *Anser caerulescens*: an effect of date or parental quality? Journal of Avian Biology 30:72-78.

Lesage, L., and G. Gauthier. 1997. Growth and organ development in Greater Snow Goose goslings. Auk 114:229-241.

Lesage, L., and G. Gauthier. 1998. Effect of hatching date on body and organ development in Greater Snow Goose goslings. Condor 100:316-325.

Lindberg, M. S., Sedinger, J. S., and Flint, P. L. 1997. Effects of spring environment on nesting phenology and clutch size of Black Brant. Condor 99:381-388.

Lindström, J. 1999. Early development and fitness in birds and mammals. Trends in Ecology and Evolution 14:343-348.

Loonen, M. J. J. E., K. Oosterbeek, and R. H. Drent. Variation in growth of young and adult size in barnacle geese *Branta leucopsis*: evidence for density dependence. Ardea 85:177-192.

MacInnes, C. D. 1962. Nesting of small Canada geese near Eskimo Point, Northwest Territories. Journal of Wildlife Management 26:247-256.

MacInnes, C. D., and E. H. Dunn. 1988. Components of clutch size variation in arctic-nesting Canada geese. Condor 90:83-89.

MacInnes, C. D., E. H. Dunn, D. H. Rusch, F. Cooke, and F. G. Cooch. 1990. Advancement of goose nesting dates in the Hudson Bay region, 1951-1986. Canadian Field Naturalist 101:33-39.

MacInnes, C. D., R. K. Misra, and J. P. Prevett. 1989. Differences in growth parameters of Ross's geese and snow geese: evidence from hybrids. Canadian Journal of Zoology 67:286-290.

Mainguy, J., J. Bêty, G. Gauthier, and J.-F. Giroux. 2002. Are body condition and reproductive effort of laying greater snow geese affected by the spring hunt? Condor 104:156-161.

Manseau, M., and G. Gauthier. 1993. Interactions between greater snow geese and their rearing habitat. Ecology 74:2045-2055.

Martin, T. E. 1995. Avian life history evolution in relation to nest sites, nest predation, and food. Ecological Monographs 65:101-127.

Mason, D. D., P. S. Barboza, and D. H. Ward. 2007. Mass dynamics of wintering Pacific black brant: body, adipose tissue, organ, and muscle masses vary with location. Canadian Journal of Zoology 85:728-736.

McAvoy, S. E., S. A. Macko, and R. S. Carney. 2003. Links between chemosynthetic production and mobile predators on the Louisiana continental slope: stable carbon isotopes of specific fatty acids. Chemical Geology 201:229-237.

McCracken, K. G., A. D. Afton, and R. T. Alisauskas. 1997. Nest morphology and body size of Ross's geese and lesser snow geese. Auk 114:610-618.

McGarigal, K., S., Cushman, and S. Stafford. 2000. Multivariate statistics for wildlife and ecology research. Springer-Verlag, New York, Inc, pp. 1-283.

McLandress, M. R. 1983. Temporal changes in habitat selection and nest spacing in a colony of Ross' and Lesser Snow Geese. Auk 100:335-343.

Meijer, T., and R. Drent. 1999. Re-examination of capital and income dichotomy in breeding birds. Ibis 141:399-414.

Menu, S., G. Gauthier, and A. Reed. 2005. Survival of young greater snow geese (*Chen caerulescens atlantica*) during fall migration. Auk 122:479-496.

Moser, T. J., and D. C. Duncan. 2001. Harvest of Ross's geese. Pages 43-54 *in* The status of Ross's geese. (T. J. Moser, Ed.) Arctic Goose Joint Venture special publication. U.S. Fish and Wildlife Service, Washington, D.C., USA, and Canadian Wildlife Service, Ottawa, Ontario, Canada.

Mowbray, T. B., F. Cooke, and B. Ganter. 2000. Snow Goose (*Chen caerulescens*). *In* Birds of North America, No. 514 (A. Poole and F. Gill, eds.). The Birds of North America, Inc., Philadelphia, PA.

Murphy, M. E. 1994. Amino acid compositions of avian eggs and tissues: nutritional implications. Journal of Avian Biology 25:27-38.

Nagy, K. A. 1987. Field metabolic rate and food requirement scaling in mammals and birds. Ecological Monographs 57:111-128.

Newton, I. 1998. Population limitation in birds. Academic Press, San Diego, CA.

Newton, I. 2006. Can conditions experienced during migration limit the population levels of birds? Journal of Ornithology 147:146-166.

Nichols, J. D., and J. E. Hines. 2002. Approaches for direct estimation of λ, and demographic contributions to λ, using capture-recapture data. Journal of Applied Statistics 29:539-568.

Nolet, B. A., and R. H. Drent. 1998. Bewick's swans refuelling on pondweed tubers in the Dvina Bay (White Sea) during their spring migration: first come, first served. Avian Biology 29:574–581.

Nur, N., and W. J. Sydeman. 1999. Survival, breeding probability and reproductive success in relation to population dynamics of Brandt's Cormorants *Phalacrocorax penicillatus*. Bird Study 46[Suppl]:92-103.

O'Brien, D. M., M. L. Fogel, and C. L. Boggs. 2002. Renewable and nonrenewable resources: Amino acid turnover and allocation to reproduction in Lepidoptera. Proceedings of the National Academy of Sciences 99:4413-4418.

Oli, M. K., and F. S. Dobson. 1999. Population cycles in small mammals: the role of age at sexual maturity. Oikos 86:557-565.

Owen, M., and J. M. Black. 1989. Factors affecting the survival of Barnacle Geese on migration from the breeding grounds. Journal of Animal Ecology 58:603-617.

Owen, M., and J. M. Black. 1990. Waterfowl Ecology. Pages 114-220. Chapman and Hall, New York.

Parker, H., and H. Holm. 1990. Patterns of nutrient and energy expenditure in female common

eiders nesting in the high Arctic. Auk 107:660-668.

Perrin, N. 1998. On body size, energy and fitness. Functional Ecology 12: 500–502.

Peters, R. H. 1983. The ecological importance of body size. Cambridge University Press, Cambridge, pp 1-329.

Petersen, M. H. 1992. Reproductive ecology of Emperor Geese: annual and individual variation in nesting. Condor 94:383-397.

Pezzanite, B. 2003. The foraging behavior of lesser snow geese and Ross's geese on La Pérouse Bay. Ph.D. Thesis. City University of New York, New York.

Phillips, D. L., and J.W. Gregg. 2003. Source partitioning using stable isotopes: coping with too many sources. Oecologia 136:261-269.

Piersma, T. 2002. Energetic bottlenecks and other design constraints in avian annual cycles. Integrative and Comparative Biology 42:51-67.

Ploeger, P. L. 1968. Geographic differentiation in arctic Anatidae as a result of isolation during the last glacial. Ardea 56:1-159.

Polischuk, S. C., K. A. Hobson, and M. A. Ramsay. 2001. Use of stable-carbon and nitrogen isotopes to assess weaning and fasting in female polar bears and their cubs. Canadian Journal of Zoology 79:499-511.

Polito, M. J., S. Fisher, C. R. Tobias, and S. D. Emslie. 2009. Tissue-specific isotopic discrimination factors in gentoo penguin (*Pygoscelis papua*) egg components: implications for dietary reconstruction using stable isotopes. Journal of Experimental Marine Biology and Ecology 372:106-112.

Post, D. M., C. A. Layman, D. A. Arrington, G. Takimoto, C. G. Montaña, and J. Quattrochi. 2007. Getting to the fat of the matter: models, methods and assumptions for dealing with lipids in stable isotope analyses. Oecologia 152:179-189.

Prop, J. 2004. Food finding: on the trail to successful reproduction in migratory geese. Ph.D. Thesis. University of Groningen, Groningen, Netherlands.

Prop, J., and J. de Vries. 1993. Impact of snow and food conditions on the reproductive performance of Barnacle geese *Branta leucopsis.* Ornis Scandinavica 24:110-121.

Prop, J., and C. Deerenberg. 1991. Spring staging in brent geese *Branta bernicula*: feeding constraints and the impact of diet on the accumulation of body reserves. Oecologia 87:19-28.

Rau, G. H., C. W. Sullivan, and L. I. Gordon. 1991. $\delta^{13}C$ and $\delta^{15}N$ variations in Weddell Sea particulate organic matter. Marine Chemistry 35:355-369.

Rayner, J. M. V. 1988. Form and function in avian flight. Current Ornithology 5:1–66.

Raveling, D. G. 1978. Dynamics of distribution of Canada geese in winter. Transactions of the 43rd N. A. Wildlife & Natural Resource Conference.

Raveling, D. G. 1978. The timing of egg laying by northern geese. Auk 95:294-303.

Raveling, D. G. 1979. The annual cycle of body condition of Canada Geese with special reference to control of reproduction. Auk 96:234-252.

Raveling, D. G. 1989. Nest-predation rates in relation to colony size of Black Brant. Journal of Wildlife Management 53:87-90.

Reed, E. T., G. Gauthier, and J.-F. Giroux. 2004. Effects of spring conditions on breeding propensity of Greater Snow Goose females. Animal Biodiversity and Conservation 27.1:35-46.

Reed, E. T., G. Gauthier, R. Pradel, and J.-D. Lebreton. 2003. Age and environmental conditions affect recruitment in greater snow geese. Ecology 84:219-230.

Reed, A., and N. Plante. 1997. Decline in body mass, size, and condition of greater snow geese, 1975-94. Journal of Wildlife Management 61:413-419.

Ricklefs, R. E. 1989. Adaptations to cold in bird chicks. Pages 329-338 *in* Physiology of cold adaptation in birds (C. Bech and R. E. Reinertsen, Eds.). Plenum Press, New York.

Ricklefs, R. E., 2000. Density dependence, evolutionary optimization, and the diversification of avian life histories. Condor 102:9-22.

Ricklefs, R. E., and M. Wikelski. 2002. The physiology/life history nexus. Trends in Ecology and Evolution 17:462-468.

Robbins, C. T., L. A. Felicetti, and M. Sponheimer. 2005. The effect of dietary protein quality on nitrogen isotope discrimination in mammals and birds. Oecologia 144:534-540.

Rockwell, R. F., E. G. Cooch, and S. Brault. 1997. Dynamics of the mid-continent population of Lesser Snow Geese-projected impacts of reduction in survival and fertility on population growth rates. Pages 73-100 *in* Arctic ecosystems in peril: report of the Arctic Goose Habitat Working Group (B. D. J. Batt, Ed). Canadian Wildlife Service, Ottawa, Ontario, and U.S. Fish and Wildlife Service, Washington, D.C.

Rohwer, F. C. 1992. The evolution of reproductive patterns in waterfowl. Pages 486–539 *in* The Ecology and Management of Breeding Waterfowl (B. D. J. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu, Eds.). University of Minnesota Press, Minneapolis.

Roth, J. D., and K. A. Hobson. 2000. Stable carbon and nitrogen isotopic fractionation between diet and tissue of captive red fox: implications for dietary reconstruction. Canadian Journal of Zoology 78:848-852.

Ryder, J. P. 1969. Nesting colonies of Ross's Goose. Auk 86:282-292.

Ryder, J. P. 1970. A possible factor in the evolution of clutch size in Ross's Geese. Wilson Bulletin 82:4-13.

Ryder, J. P. 1972. Timing and spacing of nests and breeding biology of Ross' goose. Ph.D. Thesis, University of Saskatchewan, Saskatoon, Saskatchewan.

Ryder, J. P., and R. T. Alisauskas. 1995. Ross's goose (*Chen rossii*). *In* Birds of North America, No. 162 (A. Poole and F. Gill, eds.). The Academy of Natural Sciences, Philadelphia, and The American Ornithologists' Union, Washington, D.C.

Saether, B.-E., and O. Bakke. 2000. Avian life history variation and contribution of demographic traits to the population growth rate. Ecology 81:642-653.

Saether, B.-E. T. H. Ringsby, and E. Røskaft. 1996. Life history variation, population processes and priorities in species conservation: towards a reunion of research paradigms. Oikos 77:217-226.

Sandercock, B. K., K. Martin, and S. J. Hannon. 2005. Life history strategies in extreme environments: comparative demography of arctic and alpine ptarmigan. Ecology 86:2176-2186.

Samelius G., and R. T. Alisauskas. 2001. Deterring arctic fox predation: the role of parental nest attendance by lesser snow geese. Canadian Journal of Zoology 79:861-866.

Samelius G., and R. T. Alisauskas. 2006. Sex-biased costs in nest defence behaviours by lesser snow geese (*Chen caerulescens*): consequences of parental roles? Behavioral Ecology and Sociobiology 59:805-810.

SAS Institute Inc. 2008. SAS OnlineDoc® 9.1 3 Cary, SAS Institute Inc., Cary, North Carolina.

Schmidt-Nielsen, K. 1984. Scaling, Why is Animal Size so Important? Cambridge, Cambridge University Press, pp. 1-241.

Schmutz, J. A. 1993. Survival and prefledging body mass in juvenile Emperor Geese. Condor 95:222-225.

Schmutz, J. A., K. A. Hobson, and J. A. Morse. 2006. An isotopic assessment of protein from diet and endogenous stores: effects on egg production and incubation behaviour of geese. Ardea 94:385-397.

Schmutz, J. A., B. F. Manly, and C. P. Dau. 2001. Effects of gull predation and weather on survival of Emperor goose goslings. Journal of Wildlife Management 65:248-257.

Schmutz, J. A., R. F. Rockwell, and M. R. Petersen. 1997. Relative effects of survival and reproduction on the population dynamics of emperor geese. Journal of Wildlife Management 61:191-201.

Schultz, E. T. 1993. The effect of birth date on fitness of female dwarf perch, *Micrometrus minimus* (Perciformes: Embiotocidae). Evolution 47:520-539.

Sedinger, J. S. 1984. Protein and amino acid com-position of tundra vegetation in relation to nutritional requirements of geese. Journal of Wildlife Management 48:1128-1136.

Sedinger, J. S. 1997. Adaptations to and consequences of an herbivorous diet in grouse and waterfowl. Condor 99:314-326.

Sedinger, J. S., and P. L. Flint. 1991. Growth rate is negatively correlated with hatch date in Black Brant. Ecology 72:496-502.

Sedinger J. S., P. L. Flint, and M. S. Lindberg. 1995. Environmental influence on life-history traits: growth, survival, and fecundity in black brant (*Branta bernicula*). Ecology 76:2404-2414.

Sedinger, J. S., M. S. Lindberg, M. Eichholz, and N. Chelgren. 1997. Influence of hatch date versus maternal and genetic effects on growth of Black Brant goslings. Auk 114:129-132.

Sedinger, J. S., M. S. Lindberg, B. T. Person, M. W. Eichholz, M. P. Herzog, and P. L. Flint. 1998. Density-dependent effects on growth, body size, and clutch size in black brant. Auk 115:613-620.

Sedinger, J. S., and D. G. Raveling. 1988. Foraging behavior of cackling Canada goose goslings: implications for the role of food availability and processing rate. Oecologia 75:119-124.

Sedinger, J. S., D. H. Ward, J. L. Schamber, W. I. Butler, W. D. Eldridge, B. Conant, J. F. Voelzer, N. D. Chelgren, and M. P. Herzog. 2006. Effects of El Niño on distribution and reproductive performance of Black Brant. Ecology 87:151-159.

Sinclair, A. R. E. 1989. Population regulation in animals. Pages 197-241 *in* Ecological concepts (J. M. Cherrett, Ed.). Blackwell Scientific, Oxford, UK.

Slattery, S. M. 2000. Factors affecting first-year survival in Ross's Geese. Ph.D. Thesis, University of Saskatchewan, Saskatoon, Saskatchewan.

Slattery, S. M., and R. T. Alisauskas. 1995. Egg characteristics and body reserves of neonate Ross' and lesser snow geese. Condor 97:970-984.

Slattery, S. M., and R. T. Alisauskas. 2002. Use of the Barker model in an experiment examining covariate effects on first-year survival in Ross's Geese (*Chen rossii*): a case study. Journal of Applied Statistics 29:497-508.

Slattery, S. M., and R. T. Alisauskas. 2007. Distribution and habitat use of Ross's and lesser snow geese during late brood rearing. Journal of Wildlife Management 71:2230-2237.

Speake, B. K., P. F. Surai, and G. R. Bortolloti. 2002. Fatty acid profiles of yolk lipids of five species of wild ducks (Anatidae) differing in dietary preference. Journal of Zoology London 257:533-538.

Speake, B. K., F. Decrock, P. F. Surai, and R. Groscolas. 1999. Fatty acid composition of the adipose tissue and yolk lipids of a bird with a marine-based diet, the emperor penguin (*Aptenodytes forsteri*). Lipids 34:283-290.

Stearns, S. C. 1992. The evolution of life histories. Oxford University Press, Oxford.

Stickney, A. 1991. Seasonal patterns of prey availability and the foraging behavior of arctic foxes (*Alopex lagopus*) in a waterfowl nesting area. Canadian Journal of Zoology 69:2853-2859.

Stokes, D. L., and P. D. Boersma. 2000. Nesting density and reproductive success in a colonial seabird, the megallanic penquin. Ecology 81:2878-2891.

Swick, R. W., and N. J. Benevenga. 1977. Labile protein reserves and protein turnover. Journal of Dairy Science 60:505-515.

Thomas, V. G., S. K. Mainguy, and J. P. Prevett. 1983. Predicting fat content of geese from abdominal fat weight. Journal of Wildlife Management 47:1115-1119.

Thompson, S. C., and D. G. Raveling. 1987. Incubation behavior of Emperor Geese compared with other geese: interactions of predation, body size, and energetics. Auk 104:707-716.

Todd, L. D., R. G. Poulin, T. I. Wellicome, and R. M. Brigham. 2003. Post-fledging survival of Burrowing Owls in Saskatchewan. Journal of Wildlife Management 67:512-519.

Tremblay, J.-P., G. Gauthier, D. Lepage, and A. Desrochers. 1997. Factors affecting nesting success in greater snow geese: effects of habitat and association with snowy owls. Wilson Bulletin 109:449-461.

Vanderklift, M. A., and S. Ponsard. 2003. Sources of variation in consumer-diet $d^{15}N$ enrichment: a meta-analysis. Oecologia 136:169-182.

Waddington, K., and L. MacArthur. 2008. Diet quality and muscle tissue location influence consumer-diet discrimination in captive-reared rock lobsters (*Panulirus cygnus*). Marine Biology 154:569-576.

Weller, M. V. 1956. A simple candler for waterfowl eggs. Journal of Wildlife Management 20:1111-1113.

White, G. C., and K. P. Burnham. 1999. Program MARK: Survival estimation from populations of marked animals. Bird Study 46 Supplement:120-138.

White, G. C., and E. G. Cooch. 2006. Program MARK A Gentle Introduction, 4th edition: [Online] available at phidot.org/software/mark/docs/book/

Whitehead, P. J., W. J. Freeland, and K. Tschirner. 1990. Early growth of magpie geese, *Anseranas semipalmata:* sex differences and influence of egg size. Australian Journal of Zoology 38:249-262.

Williams, T. D., E. G. Cooch, R. L. Jefferies, and F. Cooke. 1993. Environmental degradation, food limitation and reproductive output: Juvenile survival in lesser snow geese. Journal of Animal Ecology 62:766-777.

Williams, B. K., J. D. Nichols, and M. J. Conroy. 2002. Analysis and management of animal populations. Academic Press. San Diego, CA.

Wilson, H. M. 2007. Population ecology of Pacific common eiders on the Yukon-Kuskokwim Delta, Alaska. Ph.D. Thesis, University of Alaska Fairbanks, Fairbanks, Alaska.

Winkler, D. W., P. O. Dunn, and C. E. McCulloch. 2002. Predicting the effects of climate change on avian life history traits. Proceedings of the National Academy of the Sciences 99:13595-13599.

Wittenberger, J. F., and G. L. Hunt, Jr. 1985. The adaptive significance of coloniality in birds. Pages 1-78 *in* Avian Biology Volume III. (S. Farner, J. R. King, and K. C. Parkes, Eds.) Plenum Press. New York, New York.

Wypkema, R. C. P., and C. D. Ankney. 1979. Nutrient reserve dynamics of lesser snow geese staging at James Bay, Ontario. Canadian Journal of Zoology 57:213-219.

van der Jeugd, H. P., and K. Larsson. 1998. Pre-breeding survival of barnacle geese *Branta leucopsis* in relation to fledgling characteristics. Journal of Animal Ecology 67:953-996.

APPENDIX. SENSITIVITY OF INFERENCES ABOUT CAPITAL BREEDING STRATEGIES: EFFECT OF ASSUMED DISCRIMINATION FACTORS ($\Delta^{13}C$ and $\Delta^{15}N$)

A.1 INTRODUCTION

There has been an increase in the use of stable isotopes in studies about the contribution of endogenous reserves and diet items for clutch formation within migratory waterfowl (breeding strategies; Gauthier et al. 2003, Bond et al. 2007). However, successful use of stable isotopes in these studies is predicated on numerous assumptions (Hobson 1995, Gannes et al. 1998). Some of the assumptions, for example, are that dietary items must be isotopically distinct, proper tissues are selected for dietary reconstruction, and appropriate discrimination factors among diet sources and egg components are used (Gannes et al. 1998). Studies generally meet the first two assumptions because there are isotopic differences among migratory areas and breeding grounds foods within most migratory waterfowl, and there is sufficient knowledge of turnover rates in specific tissues (Gauthier et al. 2003, Bond et al. 2007). However, little is known about discrimination between diet sources with egg components (i.e., lipid-free yolk, yolk lipid, and albumen), or between endogenous reserves (i.e., breast muscle and abdominal fat) with egg components. Isotopic discrimination is the change in isotopic signature from source to product such that the ratio of heavy to light isotopes in a compound change during the process (Δ, change in isotopic ratio in parts per thousand, ‰; Post et al. 2007, Caut et al. 2008). Currently, the only available discrimination factors between diet sources and egg components in herbivorous and carnivorous birds are from Hobson (1995). There are no known discrimination factors between endogenous reserves with egg components. Consequently, many studies have utilized the carnivore model (Hobson 1995), which is based on discrimination of diet sources and egg components within falcons (*Falco spp*.) fed a meat diet, to suffice for birds mobilizing endogenous reserves for clutch formation (Gauthier et al. 2003, Schmutz et al. 2006, Bond et al. 2007). For instance, Gauthier et al. (2003) used these discrimination factors to examine the breeding strategy of greater snow geese (*Chen caerulescens atlantica*). These birds were inferred to have a predominant income strategy as they feed heavily on their breeding grounds for 14 days before initiating nests. However, Hobson (1995) surmised that these current discrimination factors were not appropriate in birds that mobilize considerable amounts of endogenous reserves

during reproduction such as Ross's geese (*Chen rossii*) and lesser snow geese (*Chen caerulescens caerulescens*, hereafter snow geese). There has also been an inconsistency in the application of discrimination factors, even for the same nutritional paths, with some studies using them (e.g., Gauthier et al. 2003, Bond et al. 2007) and others ignoring them (e.g., Hobson et al. 2004, Langin et al. 2006).

In this study, to determine the consequence of different discrimination factors on inferences about breeding strategies, I examined the sensitivity of breeding strategy estimates (proportion capital breeding) to different discrimination factors for stable carbon and nitrogen isotopes ($\Delta^{13}C$ and $\Delta^{15}N$) within two arctic goose species, Ross's and snow geese. I used Program SISUS to estimate the proportion capital breeding by varying discrimination factors to observe changes in estimates. Subsequently, I advance plausible discrimination factors for species thought to mobilize significant endogenous reserves (such as these two species of geese) and support their legitimacy based on evidence in the literature.

A.2 METHODS

A.2.1 Sample collection

This study was conducted at the Karrak Lake goose colony located in Nunavut, Canada (67° 14' N, 100° 15' W) between 4 June and 5 July, 2004 and 2005. Mean nest initiation dates in 2004 were similar to the long-term mean (1991-2005, Ross's geese = 11 June and snow geese = 9 June) for Ross's (12 June) and snow (8 June) geese, respectively (Alisauskas unpubl. data). However, in 2005 nest initiation was early for Ross's (8 June) and snow (5 June) geese.

I collected arriving adult female Ross's and snow geese with a shotgun in 2004 (8-13 June, n = 25 snow geese and n = 25 Ross's geese) and 2005 (4-14 June, n = 27 snow geese and n = 29 Ross's geese). Next, I collected early incubation adult female Ross's and snow geese with a rifle on their nest in 2004 (17-18 June, n = 23 snow geese and n = 22 Ross's geese) and 2005 (13-18 June, n = 20 snow geese and n = 21 Ross's geese). Early incubation birds were collected off their respective nests and had just commenced incubation. I subsequently collected their first and last laid eggs within a clutch (from early incubation birds only) (Gauthier et al. 2003) because I expected any differences in isotopic signatures among eggs to be greatest between these two (Schmutz et al. 2006). Laying order of eggs was determined by egg color (staining; first egg dirtiest and last egg cleanest), although if an oviducal egg (n = 2) was present in collected birds it was considered the last laid egg (Gauthier et al. 2003). I obtained nest initiation

dates by backdating incubation stage and clutch size based on mean laying intervals for these species (Ryder and Alisauskas 1995, Mowbray et al. 2000).

Birds were dissected at the field camp near Karrak Lake and samples of breast and abdominal fat were stored in 70% ethanol until preparation for stable isotope analysis (Gloutney and Hobson 1988). I removed ovaries so that developing, ovulated and atretic follicles could be counted in arrival birds. Arrival birds had their largest developing follicle or oviducal egg, if present, removed for isotopic analysis. In early incubation birds, I counted ovulated follicles, presence of oviducal eggs, and order of eggs in the nest so that the exact laying sequence of eggs could be determined (see Gauthier et al. 2003). The mean laying position of early and late laid eggs used in analyses was 1.2 and 3.5, respectively. Hereafter, early and late-laid eggs will be referred to as first and last-laid eggs. Eggs and developing follicles were boiled, placed in plastic bags, and frozen for shipment back to the laboratory. To obtain a breeding ground (exogenous) isotopic signal, I collected local food plants that were known to be consumed at Karrak Lake by either species of goose (Gloutney et al. (2001). Vegetation samples were collected within the Karrak Lake colony after birds arrived onto the colony. Vegetation was subsequently dried to a constant mass and placed in paper envelopes for shipment back to the laboratory.

A.2.2 Laboratory analyses

Samples of breast muscle, abdominal fat, egg yolk (including developing follicles), and albumen were placed in a drying oven at 60°C until constant mass was reached (Gloutney and Hobson 1998). Breast muscle and yolk samples were then subjected to successive rinses of 2:1 chloroform: methanol solution to remove lipids and were then placed under a fume hood to air dry. Liver (whole), breast, albumen, and lipid-free yolk (hereafter, yolk protein) samples were then ground to a powder with a mortar and pestal. One developing follicle or oviducal egg and 2 eggs were each analyzed from arrival and early incubation birds, respectively. Food plants available to geese at time of nesting included bearberry (*Arctostaphylos* spp.), chickweed (*Stellaria* spp.), cranberry (*Vaccinium vitis-idaea*), crowberry (*Empetrum nigrum*), Labrador Tea (*Ledum decumbens*), moss (Bryophytes), and sedge (*Carex* spp.) (Gloutney et al. 2001). Foods were ground into powder samples with a mortar and pestle. Samples of ~1 mg of goose tissues or eggs, and 2 to 5 mg of foods, were weighed into tin cups and combusted in a Europa 20:20 continuous flow ratio mass spectrometer (CFIRMS) at the Department of Soil Sciences at the University of Saskatchewan to obtain stable-carbon and stable-nitrogen isotopes ratio values. I

used laboratory standards of egg albumen and whale baleen for every 5 tissue and/or egg samples analyzed; pea-green standard was used for food sample N since vegetation has relatively low percent N. Ratios of stable isotopes were expressed in δ-notation as parts per thousand (‰) deviations from Pee Dee Belemnite ($\delta^{13}C$) and atmospheric air ($\delta^{15}N$) standards according to $\delta X = [(Rsample-Rstandard)/Rstandard] \times 1000$, where X is ^{13}C or ^{15}N and R is $^{13}C/^{12}C$ or $^{15}N/^{14}N$. Laboratory measurement error was ±0.1‰ for $\delta^{13}C$ and ±0.3‰ for $\delta^{15}N$.

A.2.3 Statistical analyses

I used program SISUS (Stable Isotope Sourcing Using Sampling, see http://StatAcumen.com/sisus) to estimate the contribution of endogenous sources (capital breeding) to clutch formation. Egg components (albumen, yolk protein and yolk lipid) of each species per year were analyzed separately in SISUS. I had three groups of estimates per species per year: (1) arrival birds with largest developing follicle and/or oviducal egg, (2) early-incubation birds with their first-laid egg in the clutch, and (3) early-incubation birds with their last-laid egg in the clutch. For arrival birds I used the mean $\delta^{15}N$ and $\delta^{13}C$ signature and standard deviation for the largest developing follicle and/or oviducal egg for egg constituents, while for early incubation birds I used the mean $\delta^{15}N$ and $\delta^{13}C$ signature and standard deviation from the first- and last-laid egg for constituents, separately. I considered the contribution of five sources to yolk protein and albumen. I used the mean and standard deviation of lipid free breast $\delta^{15}N$ and $\delta^{13}C$ signature as the endogenous source of protein (Table 4.1 in Chapter 4). For exogenous source signals, I used the mean $\delta^{15}N$ and $\delta^{13}C$ signature and standard deviation of four foods that included sedge, chickweed, moss, and shrubs (bearberry, cranberry, crowberry, and Labrador tea) (Table 4.2 in Chapter 4). Shrub genera were grouped to reduce the total number of sources since they were not an important diet item (Gloutney et al. 2001, Phillips and Gregg 2003). Further, shrub genera had similar $\delta^{13}C$ signatures ($P = 0.74$), although there were slight differences in $\delta^{15}N$ signatures ($P = 0.04$). Only ^{13}C can be measured in lipid samples because any nitrogen content is likely associated with connective adipose tissue and not part of stored triglycerides; any nitrogen associated with egg phospholipids was of too low a concentration for accurate determination of $\delta^{15}N$. The mean $\delta^{13}C$ signature and standard deviation of abdominal fat was used as a signal for endogenous contributions to yolk lipid, while the mean $\delta^{13}C$ signature of four food groups was used as the exogenous signal. For a detailed description of structuring the Bayesian mixing model (SISUS) for each mixture, see Chapter 4. I used Hobson's (1995) herbivore model for diet (local food

plants) to egg discrimination values ($\delta^{15}N$ discriminates by +3.4‰ for yolk protein and albumen, $\delta^{13}C$ discriminates by 0‰ to yolk protein and by +1.5‰ to albumen, and lipid $\delta^{13}C$ discriminates by -2.6‰ to yolk lipid) as these should be appropriate (Gauthier et al. 2003).

I examined sensitivity of my estimates (of capital contributions to egg production) by changing discrimination factors ($\Delta^{13}C$ and $\Delta^{15}N$), in whole increments, for each egg constituent separately. For yolk lipid, I varied the $\Delta^{13}C$ from -4 to +4 (i.e., $\Delta^{13}C + \delta^{13}C$ abdominal fat), while for yolk protein and albumen I considered $\Delta^{13}C$ and $\Delta^{15}N$ simultaneously and these ranged from -3 to +3, respectively (i.e., $\Delta^{13}C + \delta^{13}C$ breast muscle and $\Delta^{15}N + \delta^{15}N$ breast muscle). These values generally encompass known discrimination factors between diet and food items (e.g., Hobson 1995, Vanderklift and Ponsard 2003). Larger discrimination factors or finer increments significantly increased the number of possible combinations to examine and greatly increased computing requirements. Isotopic values of egg constituents and local foods were held constant since I was interested in the effect of changing discrimination values on estimates of breeding strategies. Data were then plotted and simple linear regression was performed to generate expected proportional capital breeding estimates for values that did not numerically converge. I fitted simple or polynomial regressions to each pair of variables (egg constituent, proportion capital breeding and discrimination factor). I judged the best fit (simple or polynomial) on the basis of the coefficient of determination (r^2).

A.3 RESULTS

Variation in presumed discrimination factors greatly influenced inferences about proportional contributions of capital vs. income-based nutrients in both species of geese. I found high sensitivities to changing discrimination factors, particularly for $\Delta^{13}C$ (Figs. A.1 to A.6); greater depletion (i.e., negative discrimination) resulted in higher estimates of proportional capital breeding (Figs. A.1 to A.6). However, there was little to no sensitivity to changing $\Delta^{15}N$ on estimates. There was also increased non-convergence of models with more depleted $\Delta^{13}C$ (<0) and more enriched $\Delta^{15}N$ (> 0) (i.e., resulting in an absence of estimates within ranges of $\Delta^{13}C$ and $\Delta^{15}N$ in Figs. A.1 to A.6). For instance, increasingly depleted $\Delta^{13}C$ or enriched $\Delta^{15}N$ placed the egg constituent outside the bivariate solution space, i.e., outside possible bounds of the food triangle for yolk protein and albumen), or outside the bounds (endpoints) of the continuum (yolk lipid) (Figs. A.7 and A.8). Overall, yolk lipid was the most sensitive to changes in discrimination factors, while albumen and yolk protein were less so.

Estimates of proportional capital breeding within yolk lipid were extremely sensitive to variable $\Delta^{13}C$, although $\Delta^{13}C$ values ≥ 0 had only modest effects on estimates. For example, the estimated increase in proportional contribution from body fat to yolk lipid by Ross's geese in 2004 was only 0.10, from +4 to 0 $\Delta^{13}C$, whereas the increase was 0.19 from 0 to -2 $\Delta^{13}C$ (Fig. A.1). Use of presumed $\Delta^{13}C$ values < -2 were often inestimable for Ross's geese (Fig. A.1). The largest change in estimates of proportional capital breeding occurred in 2005 (first-laid egg) for the +4 to -3 $\Delta^{13}C$ range when there was a 0.66 increase in capital breeding (Fig. A.1). Variation in $\Delta^{13}C$ created similar patterns in snow geese, although the influence on inferences about proportional capital breeding was greater (Fig. A.2). For example, in last eggs laid by snow geese in 2005, the estimated increase in capital breeding from +4 to 0 $\Delta^{13}C$ was only 0.18, while from 0 to -3 $\Delta^{13}C$ it increased by 0.60. Consequently, the $\Delta^{13}C$ range from +4 to -3 represented a change in estimated capital breeding of 0.78 (Fig. A.2). $\Delta^{13}C$ values < -3 precluded estimation of proportional capital breeding in yolk lipid of snow geese (Fig. A.2). In general, sensitivities to $\Delta^{13}C$ values followed similar patterns for all egg components and both species, as there were inferences for increased use of capital nutrients with depleted $\Delta^{13}C$ (Figs. A.1 and A.2).

I also found that sensitivity of inference about proportional capital breeding to yolk protein in relation to variation in presumed discrimination was similar between both species. I detected considerable nonconvergence of some estimates when using negative discrimination factors. For example, -3 and -2 $\Delta^{13}C$ with $\Delta^{15}N$ -3 to +3 never converged in Ross's geese and -1 $\Delta^{13}C$ only converged twice with 0 and +1 $\Delta^{15}N$ (Fig. A.3). Further, estimates for snow geese never converged for -3 $\Delta^{13}C$, although -2 $\Delta^{13}C$ with 0 $\Delta^{15}N$ converged twice in snow geese (Fig. A.4). There was little or no influence of variation in $\Delta^{15}N$ (Figs. A.3 and A.4). Estimates of proportional endogenous allocation to yolk protein were predominantly influenced by $\Delta^{13}C$; decreasing values of $\Delta^{13}C$ increased estimates of proportional capital breeding (Figs. A.3 and A.4). For example, snow geese (2005, arrival) with 0 $\Delta^{15}N$ displayed an increase of 0.05 in capital breeding from a $\Delta^{13}C$ +3 to +2 and an increase of 0.20 from a $\Delta^{13}C$ -1 to -2 (Fig. A.4). Considering the increment of +3 to 0 within Ross's geese (2005, first-laid egg) the estimate of proportional capital breeding changed by 0.33 (Fig. A.3).

Sensitivity of inferences about endogenous vs. exogenous contributions to albumen exhibited patterns similar to those for yolk protein. However, arriving Ross's geese (2004) responded differently to alterations in discrimination factors by displaying a concave shaped

curve (Fig. A.5a). Estimates did not converge for -3 and -2 $\Delta^{13}C$ with $\Delta^{15}N$ -3 to +3 and converged only twice for -1 $\Delta^{13}C$ with 0 and +1 $\Delta^{15}N$ (Fig. A.5) in Ross's geese. Additionally, estimates in snow geese never converged with -3 and -2 $\Delta^{13}C$ when used in conjunction with $\Delta^{15}N$ -3 to +3 (Fig. A.6). Overall, there was little effect of variable $\Delta^{15}N$ since estimates were very similar (i.e., high r^2) (Figs. A.5 and A.6). In comparison to yolk protein, there was greater influence of $\Delta^{15}N$ on nutrient allocation to albumen based on lower r^2 (Figs. A.5 and A.6). Nonetheless, variation in inferred nutrient allocation to albumen was predominantly influenced by $\Delta^{13}C$. Similar to yolk protein, reduced values of $\Delta^{13}C$ increased estimates of capital breeding within albumen (Figs. A.5 and A.6).

A.4 DISCUSSION

My assessment showed that assumptions about discrimination factors associated with contributions of endogenous nutrients to egg components can have profound influences on conclusions about breeding strategies within arctic-breeding Ross's and snow geese, presumed by Ryder (1970) and Ankney and MacInnes (1978) to have been largely capital breeders. For example, some estimates of proportional endogenous allocation to yolk lipid were as low as 0.15 (i.e., predominantly income) and as high as 1.0 (i.e., completely capital). Thus, my sensitivity analysis emphasizes that properly estimated discrimination factors are required to produce meaningful results (Roth and Hobson 2000, Caut et al. 2008). Moreover, this sensitivity analysis allowed me to assess the effect of variation in discrimination values currently used for endogenous reserves to egg constituents from Hobson's (1995) carnivore model on breeding strategies; results were highly skewed toward income breeding or were not estimated at all (i.e., nonconvergence). For example, Hobson's (1995) abdominal fat $\Delta^{13}C$ to yolk lipid of 0‰ consistently produced breeding strategies for yolk lipid suggestive of income breeding (range 0.54 to 0.79) (Figs. A.1, A.2 and A.8). Likewise, my results showed that albumen $\Delta^{13}C$ and $\Delta^{15}N$ from breast muscle of 1.5‰ and +3.4‰ produced estimates biased toward income breeding (range 0.59 to 0.80) (Figs. A.5 and A.6), though I could not directly estimate proportional nutrient allocation for albumen and yolk protein utilizing the carnivore model because I didn't consider $\Delta^{15}N > +3$. However, using +3 instead of +3.4 $\Delta^{15}N$ should have been sufficient since there was little variation in inference about breeding strategies with increasing $\Delta^{15}N$ at $\Delta^{13}C > 0$. Yolk protein to breast muscle $\Delta^{13}C$ and $\Delta^{15}N$ of 0‰ and +3.4‰ would not have numerically converged. In my models, when I used +3 $\Delta^{15}N$ only 1 out of 12 models converged (snow geese

2004 arrival) (Figs. A.3 and A.4). For these reasons, I believe the carnivore model is not suitable when studying breeding strategies of species mobilizing significant endogenous reserves (Hobson 1995). Though the carnivore model has been used in previous breeding strategy studies, target species were primarily income breeders (Gauthier et al. 2003, Schmutz et al. 2006, Bond et al. 2007). Thus, for these arctic breeding geese, discrimination factors associated with movement of endogenous nutrients to egg components must be less than discrimination factors for movement of exogenous nutrients to egg components in order to provide proper breeding strategy results.

It is well known that Ross's and snow geese store endogenous reserves during spring migration in two major episodes; nearly all fat reserves are obtained in prairie Canada, while protein reserves are acquired on northern staging areas (Wypkema and Ankney 1979, Alisauskas and Ankney 1992, Bon 1997). Female Ross's geese store 290 g of fat reserves on the prairies and 15 g of protein from departure of Canadian prairies to arrival onto breeding grounds (Bon 1997). Moreover, most species of arctic geese feed very little after arrival, during egg-laying, and incubation (Ankney and MacInnes 1978 but see Gauthier et al. 2002). In a study done at the Karrak Lake colony, Gloutney et al. (2001) documented that Ross's and snow geese forage for ~8 hr per day obtaining ~1.4 g (dry mass) of forage per hour, which equates to just 4 g of dry matter assimilation per day. In general, geese have inefficient digestive systems compared to other herbivores; consequently they must process large amounts of vegetation to meet nutrient demands for maintenance requirements, let alone reproduction (Sedinger 1997). Moreover, the quality and quantity of forage at the Karrak Lake colony may preclude adequate nutrient assimilation concurrent to egg production. For instance, Alisauskas et al. (2006) documented that little quality vegetation remains for consumption at the colony since population growth has accelerated devegetation (Gloutney et al. 2001). Nevertheless, short time lags between arrival and nest initiation may prevent geese from exploiting any breeding ground forage for clutch formation given these species initiate rapid follicle growth during late spring migration and commence egg-laying $\leq$3 d after arrival (Raveling 1978, Bon 1997, Gloutney et al. 2001). As well, Ross's and snow geese lose about 20% and 33% of their protein and fat reserves, respectively, during egg-laying (from arrival to the end of the laying period) (Traylor unpubl. data). Such large declines in nutrient reserves concurrent to egg formation suggest a strong

reliance on somatic protein and fat reserves for reproduction and energy metabolism (Le Maho et al. 1981, Cherel et al. 1988).

Reliance upon endogenous protein and fat reserves during breeding likely results in preferential mobilization of these macronutrients to clutch formation, which would lessen discrimination factors from somatic reserves to egg components. The carnivore model posits no discrimination within $\delta^{13}C$ from somatic lipid to yolk lipid (Hobson 1995). Gauthier et al. (2003) supported the use of the carnivore model in lipids since in Polar bears (*Ursus maritimus*), which store fat from seals, $\delta^{13}C$ lipid values are similar to seal lipid values (Polischuk et al. 2001). However, this reasoning may be flawed since when birds mobilize lipids for egg production it is not analogous to consumption since there likely is preferential mobilization of specific fatty acids to the yolk lipid (Speake et al. 1999, Speake et al. 2002). Fatty acids synthesized from carbohydrates are known to be depleted in ^{13}C relative to the carbohydrate diet (DeNiro and Epstein 1977), and this can influence the $\delta^{13}C$ value of the bulk tissue (Rau et al. 1991, Focken and Becker 1998). Hammer et al. (1998), in a study on Redhead ducks (*Aythya americana*), found variation in fatty acid signatures and consequently suggested that there were metabolic discriminations associated with the catabolism of the different fatty acids. Moreover, Abrajano et al. (1994) observed greater depletion in ^{13}C of fatty acids with increasing degree of unsaturation; some studies have documented a depletion of ~2‰ in $\delta^{13}C$ values when fatty acids were desaturated (Deniro and Epstein 1977, McAvoy et al. 2003). Unsaturated fatty acids are highly labile and are mobilized as an energy source during migration and reproduction (Johnston 1973, Heitmeyer and Fredrickson 1990, Hammer et al. 1998). For instance, Parker and Holm (1990) found that common eiders (*Somateria mollissima borealis*), which fast during breeding, preferentially mobilized fatty acids such as 18:1 (Oleic, unsaturated), 16:0 (Palmitic, saturated), 16:1 (Palmitoleic, unsaturated) for lipid catabolism. Likewise these fatty acids, which are esterified in the liver, are prominent in yolk triacylglycerol and phospholipid of eggs of five species of wild ducks (Speake et al. 2002). Thus, if fatty acids vary in $\delta^{13}C$ signature and if there is preferential mobilization or desaturation of fatty acids allocated from abdominal fat to yolk lipid, discrimination may be significantly less than zero.

The carnivore model further argues against lipid discrimination by stating "lipids in quail muscle are depleted by 3.2‰ relative to lipid free muscle, a value almost identical to the mean depletion of yolk lipid relative to lipid-free quail muscle. This suggests that yolk lipids are

derived without discrimination either from diet or lipid stores." (Hobson 1995). Though, I do not have $\delta^{13}C$ values for lipids from breast muscle, an analogous comparison would be to take the difference between yolk lipid and abdominal lipid in my geese. When this is done mean values are between -3.28 and -3.64; consequently this suggests discrimination values less than the carnivore model (Fig. A.9). Indeed, recent results from DeVink (2007) suggest a -2.5 $\delta^{13}C$ lipid discrimination from somatic lipid to yolk lipid in breeding white-winged scoters (*Melanitta fusca*). I think that a -3.2 ^{13}C discrimination factor for abdominal fat to yolk lipid is more plausible than no discrimination (Table 1 in Hobson 1995); utilization of a -3.2 $\Delta^{13}C$ would generate estimates indicative of substantial reliance on somatic lipid for clutch formation (Figs. A.1 and A.2).

Discrimination factors from somatic reserves to egg components for ^{15}N are also probably substantially less for capital breeders than current values used by the carnivore model. The carnivore model assumes a large +3.4 discrimination factor for ^{15}N breast tissue to yolk protein and albumen. This value creates substantial disparity in nitrogen values among breast and egg components which biases nutrient allocation strategies toward income breeding (Fig. A.7). Hobson (1995) argued that considerable discrimination is apparent because "protein synthesis and its corresponding isotopic discrimination for egg components is similar to the synthesis of other proteins in birds" and "$\delta^{15}N$ discrimination occurs during amino acid amination and transamination". However, I think that once $\delta^{15}N$ discrimination occurs upon initial incorporation into tissues there is little chance for further discrimination (e.g., mobilization of amino acids to egg protein) (Felicetti et al. 2003). I propose that preferential mobilization of endogenous protein to egg protein is analogous to protein metabolism where proteins are broken down into component amino acids. For instance, muscular sarcoplasm, within the breast muscle, functions as the predominant source of labile amino acid reserves accessed during reproduction (Kendall et al. 1973, Houston et al. 1995, Cottam et al. 2002). It is known in snow geese that breast muscles serve as a consistent, reliable protein reserve for clutch formation (Ankney and MacInnes 1978) because the amino acid content within eggs and breast muscles are similar with the exception of sulfur amino acids (MET and CYS/2) (Murphy 1994, Cottam et al. 2002). Mobilization of endogenous protein to egg protein is likely achieved through constant turnover of muscle tissues which provides a continuous supply of amino acids (Swick and Benevenga 1977).

Other factors such as dietary protein quality, C:N variability, and nutritional stress may be additional determinants limiting $\Delta^{15}N$ from breast to egg components. In general, $\Delta^{15}N$ decreases as dietary protein quality increases (Adams and Sterner 2000, Roth and Hobson 2000, Robbins et al. 2005). For instance, Fantle et al. (1999) found that Atlantic blue crabs (*Callinectes sapidus*) fed a high protein diet only experienced a +0.1 $\Delta^{15}N$ into their tissues. Likewise, breast proteins of Ross's and snow geese are of high quality with C: N ratios being ~3.3 for both species. C: N ratios index the quality of protein with lower numbers indicating greater protein quality; values of 4.0 suggest very low lipid content (i.e., high protein quality) (Robbins et al. 2005, Post et al. 2007). There may also be a relationship with C: N ratio and discrimination if there is variability among C: N ratios in diet items. For instance, Caut et al. (2008) suggested that large differences in C: N ratios of diet items cause increased discrimination. I observed no large differences between breast, albumen, and yolk protein C: N ratios; all were composed of high quality protein (Tables 4.1 and 4.2 in Chapter 4). Finally, there may be little $\Delta^{15}N$ during periods of nutritional stress (i.e., nitrogen-limited conditions such as fasting during breeding) because mass balance ensures when all of a source (breast muscle) is changed into product (egg protein) the $\delta^{15}N$ value of both is identical (i.e., no $\Delta^{15}N$) (Adams and Sterner 2000). Recall that snow and Ross's geese are concurrently drawing on limited somatic reserves for energy and reproductive metabolism once arriving at the colony. Thus, these geese, likely experience modest discrimination of nitrogen from endogenous stores to egg protein because they have high nitrogen use efficiency (Le Maho et al. 1981, Cherel et al. 1988, but see Boismenu et al. 1992). Accordingly, I think that $\Delta^{15}N$ from somatic tissue to egg tissue is less than a value of +3.4; a more suitable value is +0.87 from Vanderklift and Ponsard's (2003) recent meta-analysis on $\Delta^{15}N$. Use of +0.87 $\Delta^{15}N$ would lead to estimates that support inference of substantial reliance on somatic protein for clutch formation (Figs. A.3, A.4, A.5, and A.6).

The last set of discrimination factors from the carnivore model are for lipid-free $\delta^{13}C$ breast to yolk protein and albumen. The carnivore model suggests 0 and +0.9 $\delta^{13}C$ discrimination from breast to yolk protein and albumen, respectively. However, I think that discrimination values for these components in capital breeders are probably less. For instance, Felicetti et al. (2003) suggested additional ^{13}C discrimination since it changes forms in the body, though O'Brien et al. (2002) found that egg amino acids displayed little $\delta^{13}C$ discrimination in hawkmoths (*Amphion floridensis*), and suggested that this results because storage proteins serve

as a source of C. Because amino acids from breast muscles are the probable protein source, I think that a value of -0.1 for both components is more plausible. For instance, Fantle et al. (1999) documented experimentally for Atlantic blue crabs fed a protein diet (i.e., zooplankton) that bulk amino acid (i.e., essential and non-essential amino acids) discrimination into tissues was -0.1. This value is also similar to diet-yolk protein discrimination in Mallards (*Anas platyrynchos*) in Hobson's (1995) herbivore model.

Currently, there are no known discrimination factors between endogenous reserves with egg components. My results suggest that use of discrimination factors from the carnivore model may not be suitable for capital breeders; discrimination factors from the carnivore model made breeding strategies from these geese inestimable or $\geq$ income breeders than greater snow geese, which arrive and feed for ~14 days before nesting. I admit obtaining discrimination factors from laboratory based experiments would be preferred; though inducing starving birds such as these geese to lay eggs is likely impossible (Hobson 1995, Gauthier et al. 2003). However, emperor penguins (*Aptenodytes forsteri*) may be a suitable model given they produce eggs entirely from somatic tissues while fasting in the wild and they have bred in captivity (Groscolas 1986, Kirkwood and Robertson 1997). A recent study examined discrimination factors from tissues to eggs in gentoo penguins (*Pygoscelis papua*); this species which is smaller than the emperor penguin and had an income biased breeding strategy (Polito et al. 2009). Consequently, discrimination factors in this species were similar to Hobson's (1995) carnivore model (Polito et al. 2009). Studies examining species thought to mobilize significant endogenous reserves for breeding should consider employing sensitivity analyses to examine the effect of varying discrimination factors. I suspect discrimination from avian somatic tissue to egg components is less than discrimination factors for association of dietary nutrients to egg components (carnivore model). Discrimination factors I put forth from the literature produced plausible results for my species suggesting that they are largely capital breeders, which were in agreement with where birds store reserves (fat and protein) as well as developmental rates of egg constituents (Wypkema and Ankney 1979, Alisauskas and Ankney 1992a,b, Bon 1997). Ultimately, this study underscores the need for study-specific discrimination factors as their applicability depends upon numerous factors (i.e., physiological condition, diet type, habitat type, tissue, species) and additionally may show individual variation within species (Vanderklift and Ponsard 2003, Dalerum and Angerbjörn 2005, Caut et al. 2008).

Figure A.1. Inferred proportion of yolk lipid from stored body reserves of female Ross's geese in relation to variable Carbon ($\Delta^{13}C$, ‰) discrimination factors in 2004 and 2005 at Karrak Lake, Nunavut. Shown are inferred proportional allocations of somatic tissue to a) largest developing follicle or oviducal egg of arriving, and b) first or c) last eggs within a clutch of incubating females.

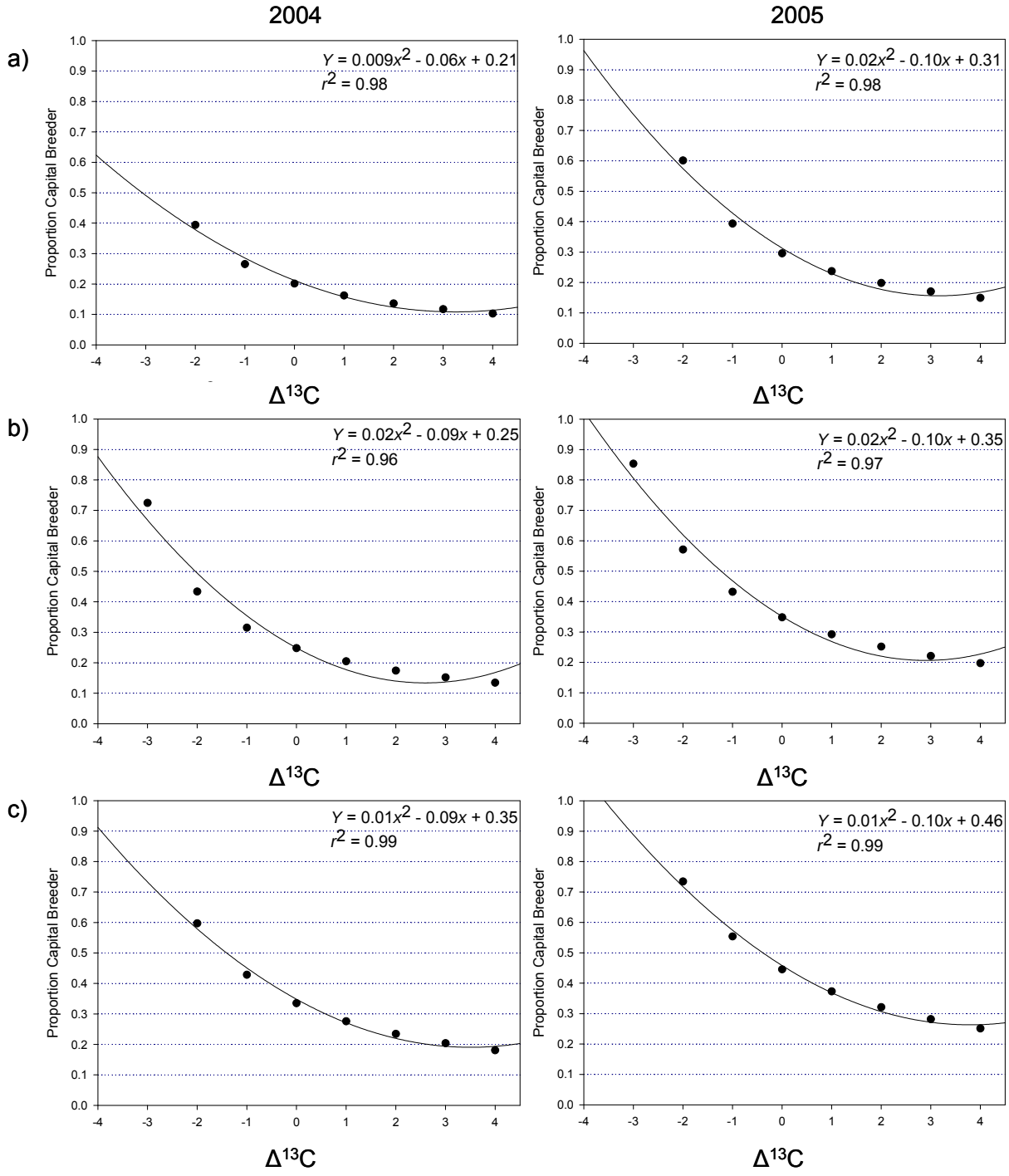


Figure A.2. Inferred proportion of yolk lipid from stored body reserves of female snow geese in relation to variable Carbon ($\Delta^{13}C$, ‰) discrimination factors in 2004 and 2005 at Karrak Lake, Nunavut. Shown are inferred proportional allocations of somatic tissue to a) largest developing follicle or oviducal egg of arriving, and b) first or c) last eggs within a clutch of incubating females.

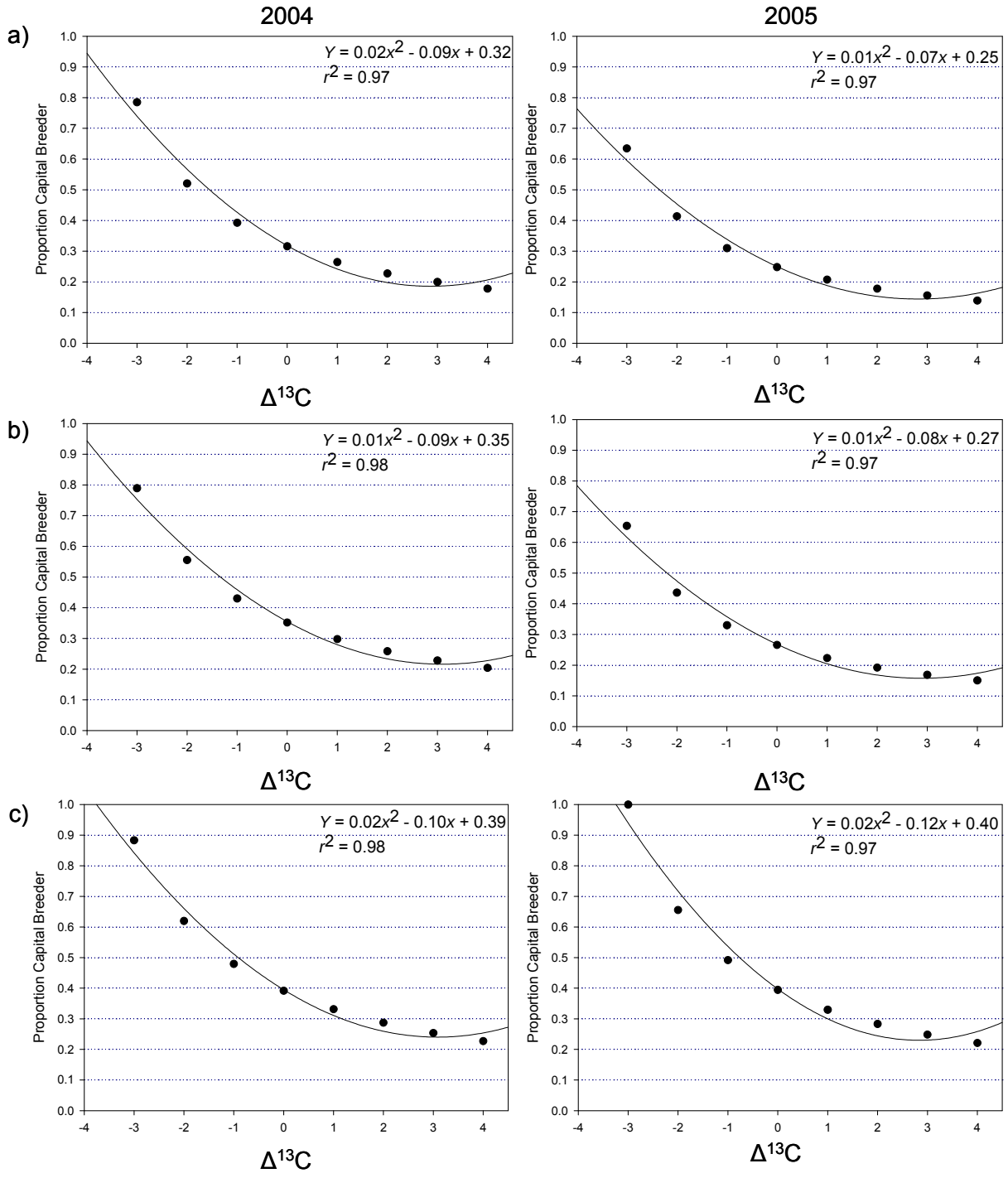


Figure A.3. Inferred proportion of yolk protein from stored body reserves of female Ross's geese in relation to variable Carbon ($\Delta^{13}C$, ‰) Nitrogen ($\Delta^{15}N$, ‰) discrimination factors in 2004 and 2005 at Karrak Lake, Nunavut. Shown are inferred proportional allocations of somatic tissue to a) largest developing follicle or oviducal egg of arriving, and b) first or c) last eggs within a clutch of incubating females.

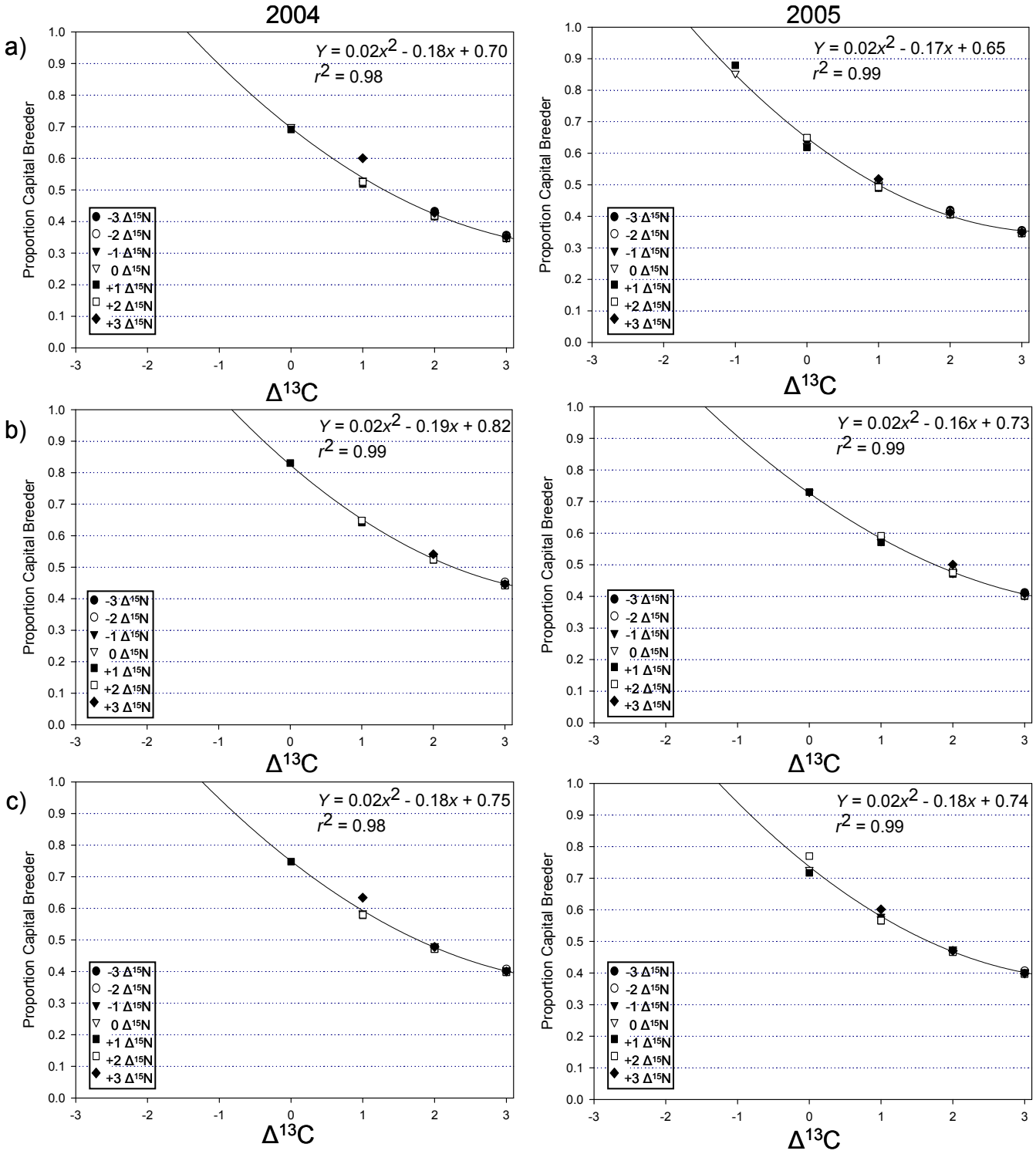


Figure A.4. Inferred proportion of yolk protein from stored body reserves of female snow geese in relation to variable Carbon ($\Delta^{13}C$, ‰) Nitrogen ($\Delta^{15}N$, ‰) discrimination factors in 2004 and 2005 at Karrak Lake, Nunavut. Shown are inferred proportions of capital breeding for a) largest developing follicle or oviducal egg of arriving, and b) first or c) last eggs within a clutch of incubating females.

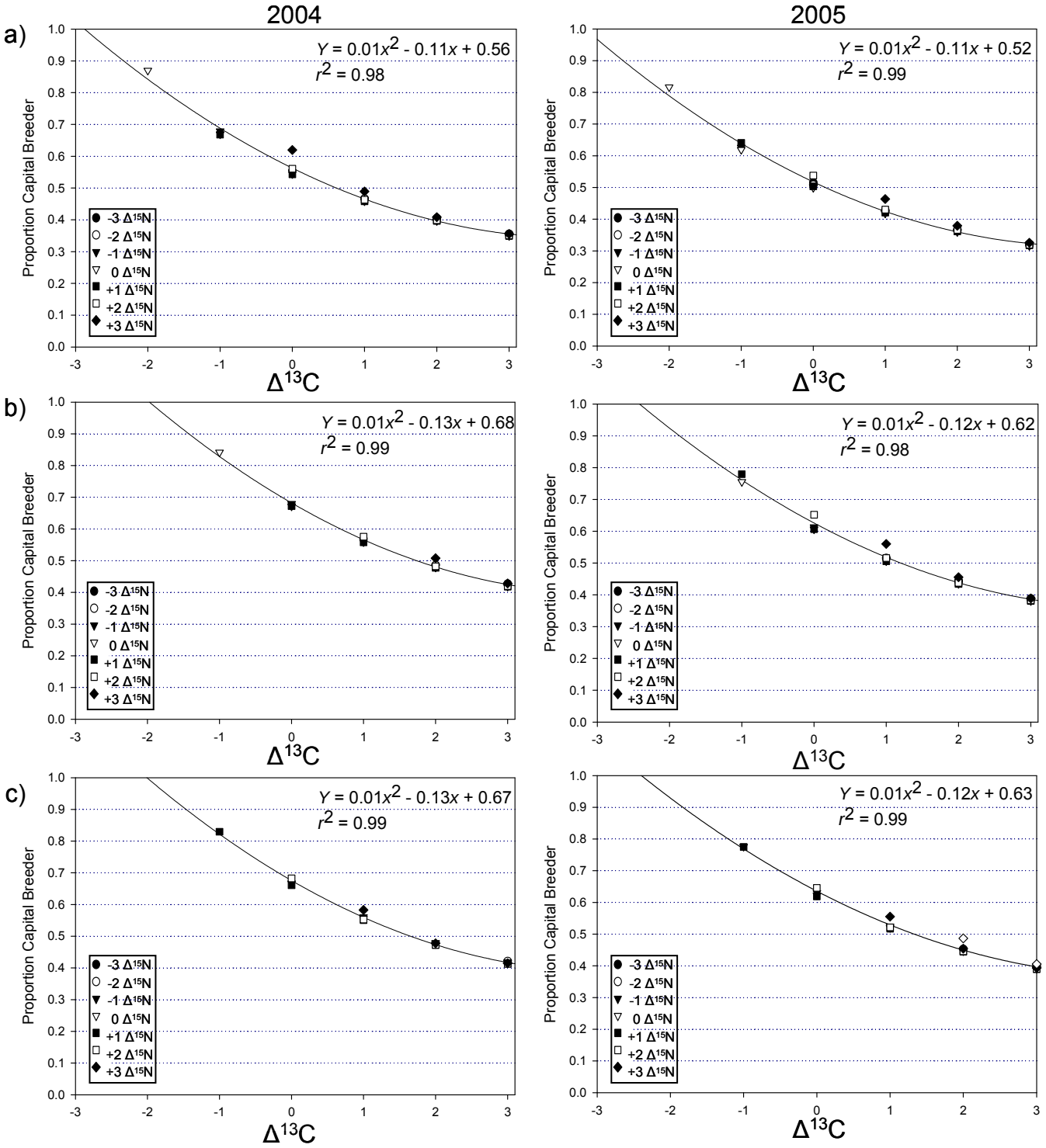


Figure A.5. Inferred proportion of albumen from stored body reserves of female Ross's geese in relation to variable Carbon ($\Delta^{13}C$, ‰) Nitrogen ($\Delta^{15}N$, ‰) discrimination factors in 2004 and 2005 at Karrak Lake, Nunavut. Shown are inferred proportions of capital breeding for a) largest developing follicle or oviducal egg of arriving, and b) first or c) last eggs within a clutch of incubating females.

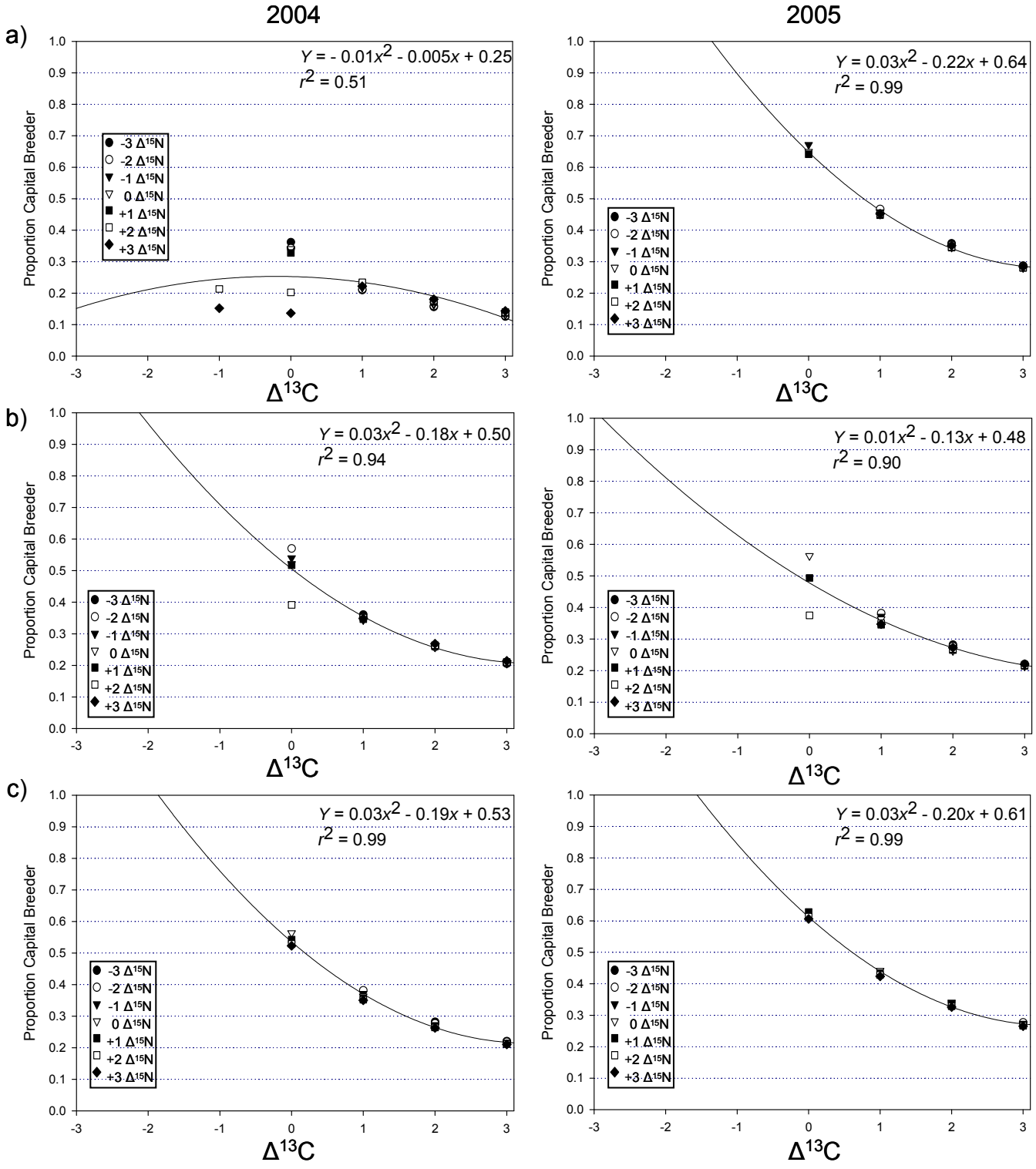
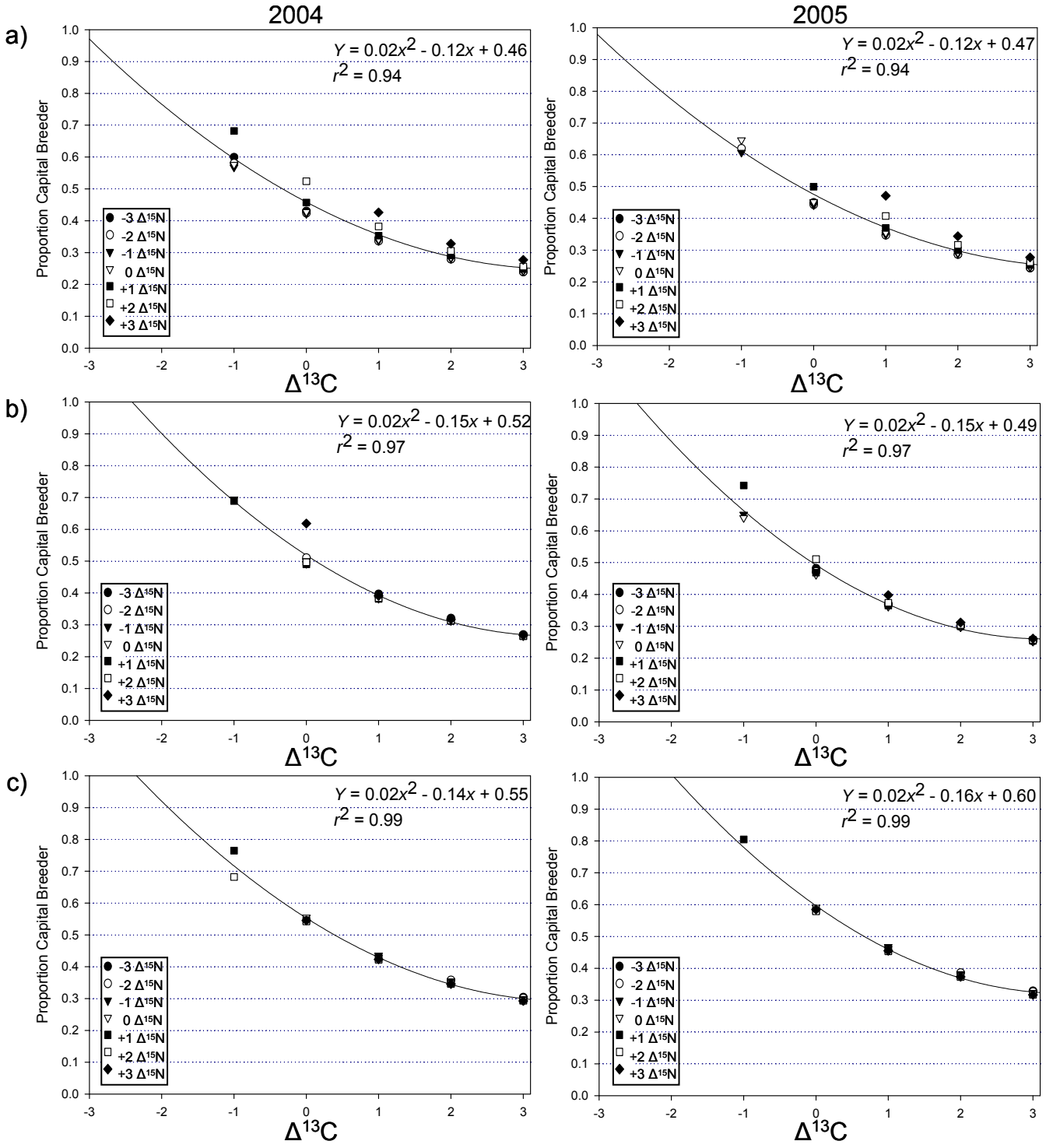
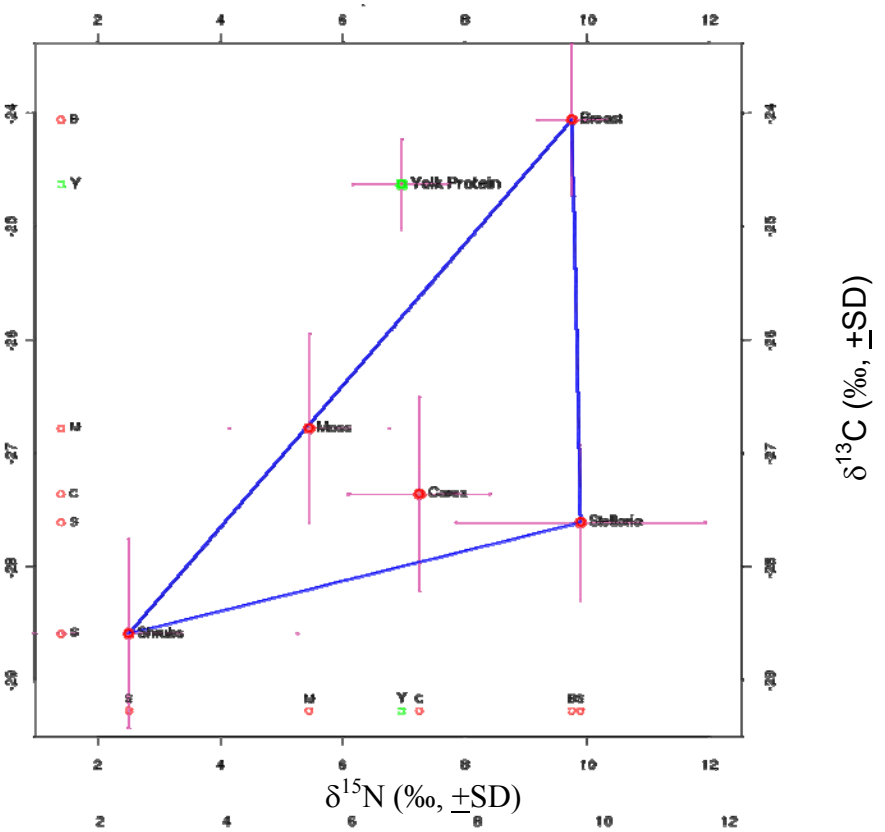


Figure A.6. Inferred proportion of albumen from stored body reserves of female snow geese in relation to variable Carbon ($\Delta^{13}C$, ‰) Nitrogen ($\Delta^{15}N$, ‰) discrimination factors in 2004 and 2005 at Karrak Lake, Nunavut. Shown are inferred proportions of capital breeding for a) largest developing follicle or oviducal egg of arriving, and b) first or c) last eggs within a clutch of incubating females.




Breast
Yolk Protein
Moss
Carex
Stellaria
Shrubs
δ15N (‰, ±SD)
δ13C (‰, ±SD)

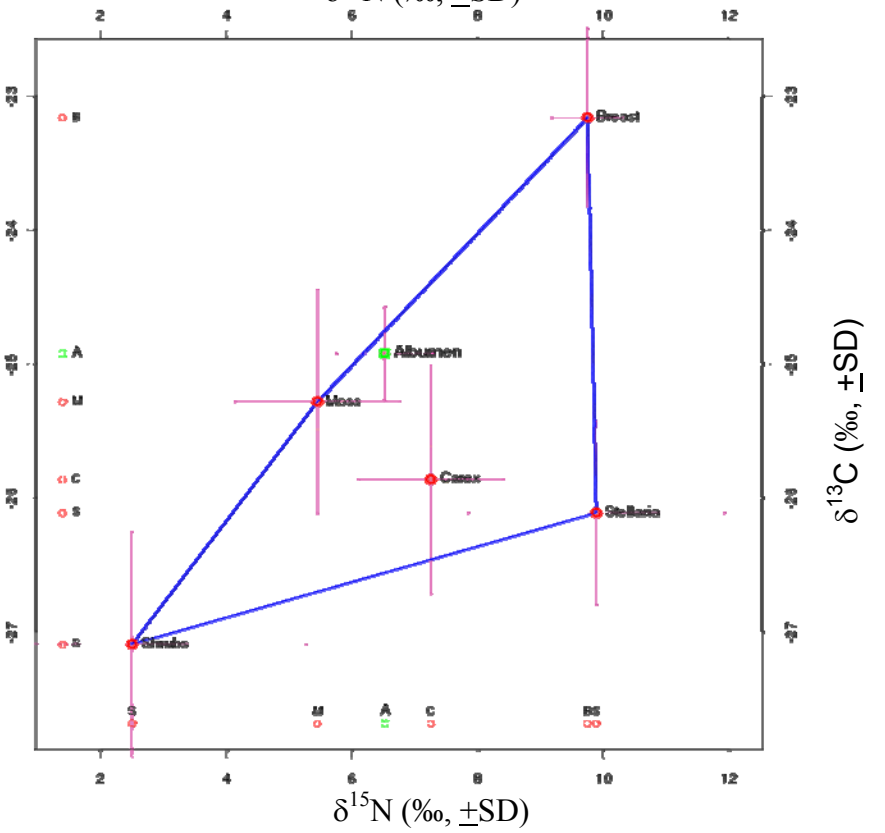

Breast
Albumen
Moss
Carex
Stellaria
Shrubs
δ15N (‰, ±SD)
δ13C (‰, ±SD)

Figure A.7. Examples of isotopic mixing source triangles for a) yolk protein and b) albumen (mixtures) when using carbon and nitrogen discrimination factors ($\Delta^{13}C$, ‰ and $\Delta^{15}N$, ‰) from the carnivore model (yolk protein $\Delta^{13}C$ and $\Delta^{15}N$ from breast muscle of 0‰ and +3.4‰, albumen $\Delta^{13}C$ and $\Delta^{15}N$ from breast muscle of 1.5‰ and +3.4‰; Hobson 1995). Food plants of Stellaria (chickweed), Carex (sedges), Bryophytes (mosses), and Shrubs [bearberry (*Arctostaphylos spp*.), cranberry (*Vaccinium vitis-idaea*), crowberry (*Empetrum nigrum*), Labrador Tea (*Ledum decumbens*)] have discrimination factors from the herbivore model (Hobson 1995) applied to their mean isotopic values. Isotopic mixing convex hulls were developed in program SISUS (Erhardt et al. unpubl. manuscript).

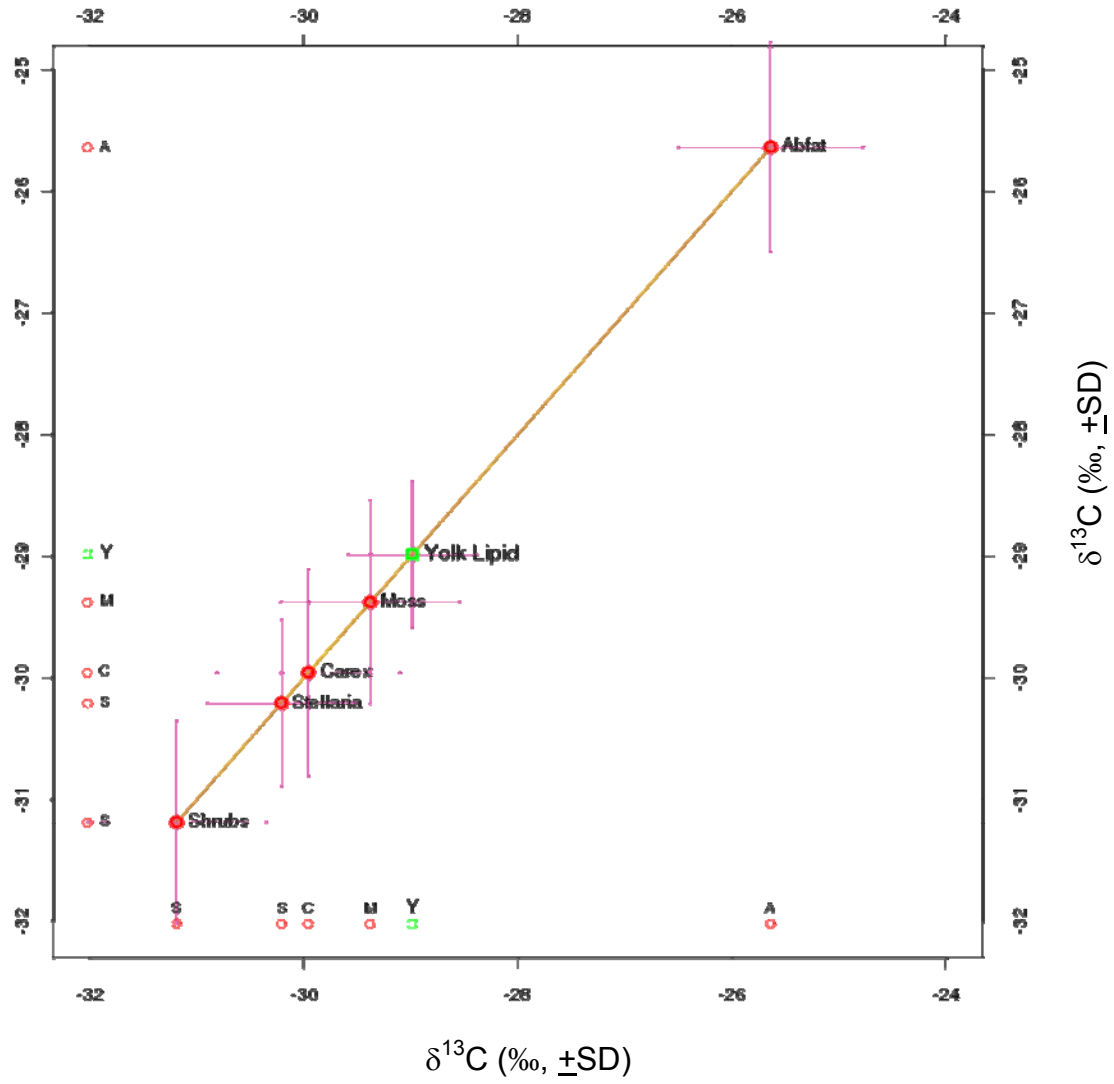


Figure A.8. An example of an isotopic mixing source continuum for yolk lipid (mixture) when using a carbon discrimination factor ($\Delta^{13}C$, ‰) from the carnivore model (abdominal fat $\Delta^{13}C$ to yolk lipid of 0‰; Hobson 1995). Food plants of Stellaria (chickweed), Carex (sedges), Bryophytes (mosses), and Shrubs [bearberry (*Arctostaphylos spp.),* cranberry (*Vaccinium vitis-idaea*), crowberry (*Empetrum nigrum*), Labrador Tea (*Ledum decumbens*)] have discrimination factors from the herbivore model (Hobson 1995) applied to their mean isotopic values. Isotopic mixing convex hull was developed in program SISUS (Erhardt et al. unpubl. manuscript).

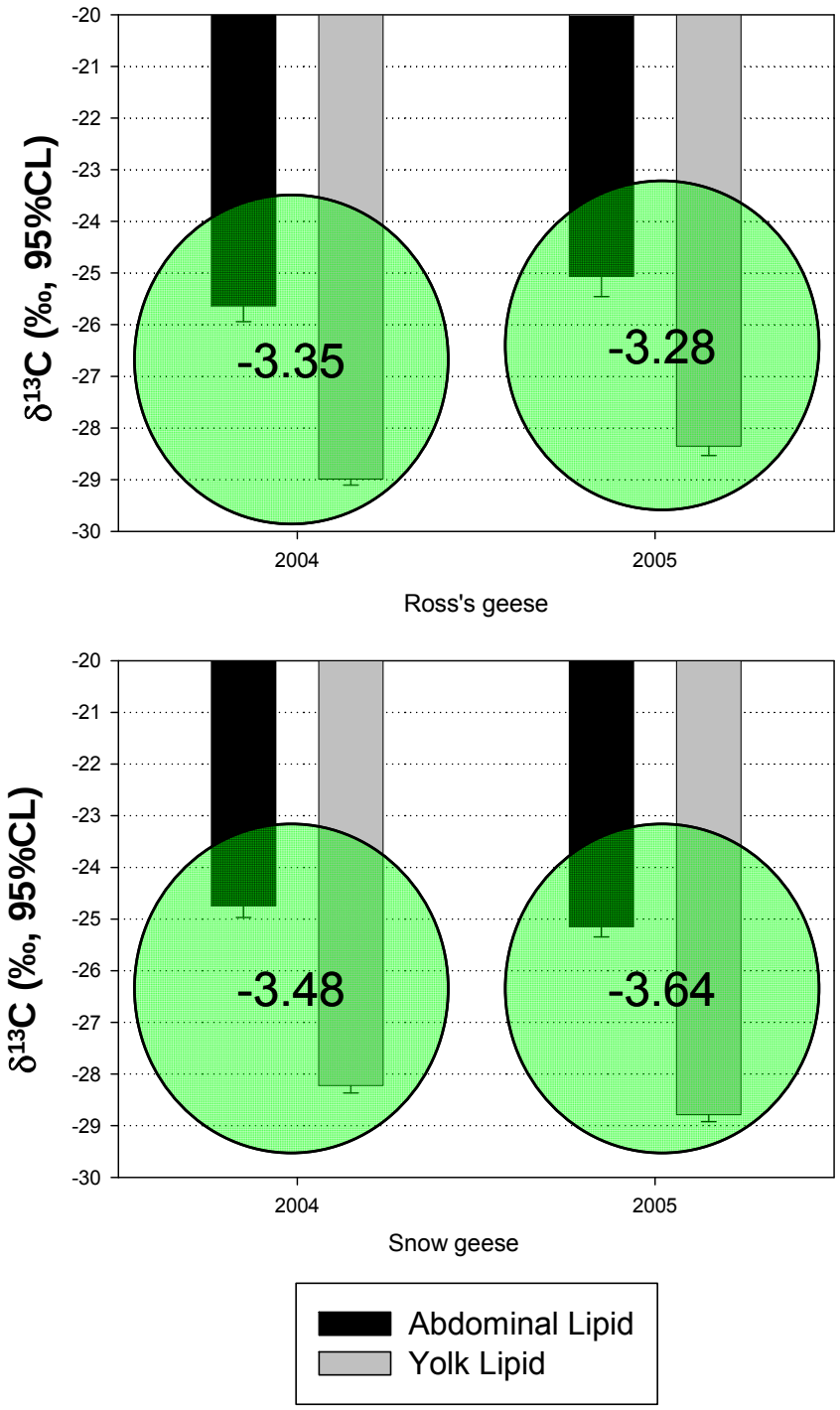


Figure A.9. Difference among mean $\delta^{13}C$ values of abdominal fat and yolk lipid (first-laid egg within a clutch) for Ross's and snow geese collected during early incubation in 2004 and 2005. Numbers within circles represent additional isotopic discrimination suggested for allocation of lipids from abdominal fat to yolk lipid.